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ALEXANDER DYAR MACGILLIVRAY.

Dr. Alexander Dyar MacGillivray, a charter member, a fellow, and former secretary-treasurer of the Entomological Society of America, died suddenly at his home in Urbana, Illinois, on March 24, 1924. He was a distinguished student of insect morphology, an authority on the Tenthredinoidea, a leading investigator of the morphology and taxonomy of immature insects and a well-known student of the Coccidæ.

For the past thirty-three years he was a teacher of entomology. Born at Inverness, Ohio, July 15, 1868, he attended Wooster College and Cornell University, graduating from the latter institution with the Ph. B. degree in 1900 and as Doctor of Philosophy in 1904. For ten years previous to graduation he was an assistant at Cornell, then instructor and assistant professor until 1911. On the latter date he went to the University of Illinois where he was successively assistant professor, associate professor and professor of systematic entomology until the time of his death.

He was the author of about eighty entomological papers dealing chiefly with external morphology and the classification of immature insects, Thysanura, Coccidæ, and Tenthredinoidea.

His monographic treatise of the Coccidæ appeared in 1921 and "External Insect Anatomy" in 1923. His private collection of sawflies contained over 400 type specimens and about 1000 species. His graduate students have made conspicuous contributions to our knowledge of the morphology of adult and immature insects.

Professor MacGillivray will be remembered by his many friends for his devotion to entomological work, for his tenaceous adherence to high scholarship, for his zeal in research, for his masterly knowledge of his special fields, and for his modesty, kindliness and unblemished character.

THE FRENULUM AND ITS RETINACULUM IN THE LEPIDOPTERA.

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I. INTRODUCTION.

The present study was undertaken with the idea that characters, so pre-eminently lepidopterous as the frenulum and its retinaculum, might throw some light on phylogenetic relationships in the Lepidoptera, if the progress of their development and specialization within the order were traced.

In an earlier paper (Braun, 1919) the writer pointed out that the series of spines on the costa of the hind wing near the base, present in Trichoptera and the more primitive Lepidoptera is not homologous with the true frenulum spines of the higher Lepidoptera, and limited the use of the term frenulum to those spines which are situated on the costal sclerite of the hind wing. To this other series of spines on the hind wing the name costal spines was applied. Failure to distinguish between these two different series of spines is apparent in the published observations of several writers, among them Tillyard (1918) and Busck (1914). As a result, conclusions are based on the erroneous assumption that a single structure is being dealt with throughout the Lepidoptera. The actual fact is, that in the process of phylogenetic development, the function of the costal

spines of the hind wing is taken over by the frenulum spines. Occasionally the costal spines and frenulum spines are present and function at the same time. Accompanying this replacement in function, there is in the fore wing a loss of some of the structures concerned in the more primitive modes of wing-coupling, the modification of others to suit new functions, and the development of new structural adaptations. The modifications of these older structures and the newer structures form the retinacula for the frenulum spines. It is with the phylogenetic origin and development of the retinacula that the present paper chiefly deals. For comparison, means of wing-coupling, such as the costal spines of the hind wing, more primitive than the frenulum, are introduced into the discussion because they seem to explain the origin and early function of the subdorsal retinaculum.

The general structure of the frenulum and its retinaculum is well known. More detailed studies of the relations of the structures and their interaction have been made by Tillyard (1918) and by A. J. Turner quoted by Tillyard (1919b). The spines referred to by Tillyard as frenulum spines in the Micropterygidæ are not homologous with the true frenulum spines of the Frenatæ, but are the spines which I have termed costal spines. Both writers recognize the difference in position and structure between the male and female retinacula in most groups of Lepidoptera and apply the terms subcostal and subdorsal to the male and female retinacula respectively.

The terms subcostal and subdorsal retinaculum adopted by Tillyard (1919b) are here used in the descriptions of these structures. The subcostal retinaculum develops commonly from the lower side of subcosta of the fore wing, sometimes from costa, sometimes from the wing membrane between the two, and as will be seen, may vary in structure and is not confined to the male alone. The subdorsal retinaculum consists of a tuft of hairs or scales placed near the base of cubitus of the fore wing, generally between Cu_1 and Cu_2.* (Fig. 6.). On the following pages, where the subdorsal retinaculum is referred to without further qualifying description, it agrees with the

*Throughout this paper, the cubitus is regarded as three-branched, the first dichotomy being into Cu_1 and Cu_2; Cu_1 dividing again into Cu_1a and Cu_1b. Cu_2 is thus the first anal of Comstock.

above definition in general character and position. The subdorsal retinaculum is usually present in both sexes, in the female often the only functional catch for the frenulum spines; in some females, it has been replaced by a functional subcostal retinaculum or by other structures acting as a specialized retinaculum for the female frenulum spines.

The present paper deals chiefly with the frenulum and its retinaculum in both sexes in the more generalized families of the Lepidoptera, with special reference to the so-called Microlepidoptera. The brief references to other families are based in large part on the work of other observers. Except in a few instances, the limits of the families are those most generally accepted.

Probably the outstanding feature of these observations is the uniformity in structure of the male retinaculum or frenulum-hook throughout the order. It is rare to find any essential deviation from the general type. The same uniformity in structure of the subdorsal retinaculum may be observed; but in the female other retinacula have developed in the course of evolution.

II. The Wing-coupling Apparatus of the Lepidoptera.

a. Micropterygidæ.

The family name is here used in its broader sense, including in the one family, the subfamilies Micropteryginæ, Eriocraniinæ and Mnesarchæinæ, which are sometimes given family rank.

In the entire group, the true frenulum spines consist of a bunch of weak, functionless bristles; in *Mnesarchæa* they are considerably longer than in the other genera. The actual wing-coupling has brought about other structures. Tillyard (1918, 1918a, 1919, 1919a) has described for the Micropteryginæ and Mnesarchæinæ the action of the jugal lobe in serving as a retinaculum for the costal spines (referred to as a frenulum);* Philpott (1922) describes in *Mnesarchæa* a specialized wing-coupling apparatus consisting of interlocking marginal hairs on the dorsal and costal margins of fore and hind wings respectively. Comstock has described the action of the jugal lobe or fibula in the Erio-

* In a recent paper, Philpott has shown that the jugal lobe functions in the Micropteryginæ as in the Eriocraniinæ, and does not serve as a retinaculum for the costal spines, which here take a backwardly oblique course and press against the inwardly curved dorsal area of the fore wing ("The Wing-coupling Apparatus in Sabatinca and other Primitive Genera of Lepidoptera," Rep. Aus. A. A. S., Vol. 16 pp. 414-419, 1923).

craniinæ as pressing down on the anterior tuberosity of the hind wing. In *Mnemonica* of the Eriocraniinæ, the costal spines project forward lying against the underside of the fore wing, but there is no indication of any holding structure, such as is shown to be present in other groups retaining functional costal spines, unless the prominent base of cubitus may be regarded as such.

The specialized wing-coupling apparatus of the Hepialidæ, which is an end group in development, has no bearing on the present discussion.

b. Nepticulidæ.

This family is of interest because in the female functional costal spines, and in some genera, a fibula, have been preserved, and at the same time, in the male, a single-spined frenulum has been attained.

In the males throughout the family, there is a strong single-spined frenulum, which catches into a well-developed subcostal retinaculum; this is in most cases the only functional wing-coupling apparatus found. The retinaculum consists of a row of looped, linear, and heavily chitinized scales inserted in sockets on the subcostal vein of the fore wing (Fig. 1). Each scale is obliquely placed and forms a loop, its free end curving almost back to subcosta; the whole forms a very efficient catch for the frenulum spine. In some forms, particularly the more specialized species of *Nepticula*, there is a slight flap-like outgrowth, or overfolding from subcosta, to the free edge of which the curved linear scales, correspondingly reduced in length, are attached.

Although the fibula is retained in the female in the primitive genera, the effective wing-coupling in the female is brought about by the catching of the costal spines of the hind wing into a subdorsal retinaculum consisting of a series of strong, heavily chitinized linear scales on the fore wing (Fig. 2). The costal spines in the female in this family are longer, stronger and more distinctly hooked at their tips than in any other group of the Lepidoptera (except the genus *Opostega*). The scales into which they catch are inserted into large scale sockets arranged in two rows parallel to Cu_2 near its base. These scales are directed very obliquely forward and outward. The subdorsal retinaculum is found in almost all females, and also persists in some males, especially in those few, such as the male of *Nepticula rhamnicola*, in which the costal spines retain their function. The thickened, roughened under surface of the first anal vein may also serve to catch the costal spines in case they become disengaged from the retinaculum.

In females of some of the more specialized species of *Nepticula*, there is the beginning of a subcostal retinaculum. A row of linear scales shorter than those of the male and usually not curved, occupies the same position as the functional retinaculum of the male. In one species, *Nepticula pteliæella*, in which these scales are curved, there is no subdorsal retinaculum, and it seems that a subcostal retinaculum has taken the place of the subdorsal retinaculum as a catch for the costal spines in the female.

c. Frenatæ.

1. Incurvariidæ.

Four genera in this family (*Chalceopla*, *Lampronia*, *Greya* and *Isocorypha*) were examined, and show considerable variation and progressive advance in specialization in wing-coupling apparatus within the family. In *Chalceopla*, the single-spined frenulum of the male is caught in a retinaculum arising from the wing membrane between costa and subcosta. This unspecialized frenulum-hook is a broad, nearly semi-circular chitinous flap, with its free rounded margin curving slightly toward the wing, just below subcosta, and clothed with curved scales. In *Lampronia* the frenulum-hook arises from a long ridge extending from subcosta obliquely across the wing membrane between subcosta and costa; its free end extends well beyond subcosta and curves toward the wing membrane. In *Greya* the frenulum-hook is an outgrowth from costa, lying in close contact with the wing membrane between costa and subcosta, then narrowing and arching up over subcosta. Its free end beyond subcosta curves abruptly toward the wing membrane. In *Isocorypha* the frenulum-hook is a long, very broadly triangular outgrowth from costa, extending one-fourth the wing length, its long distal free margin curving toward the wing (Fig. 3, ♂).

The females show a gradation from functional costal spines catching against cubitus of the fore wing as the only holding structure, to a three-spined functional frenulum held under a subcostal retinaculum consisting of broad scales and a tuft of hair-like scales. In *Chalceopla* the costal spines are preserved in primitive condition with no subdorsal retinaculum. The frenulum spines in *Chalceopla cyanella* are minute and functionless. In *Greya subalba* the costal spines are beginning to lose their characteristic form, and the frenulum spines are lengthening; a condition apparently in which there is no very effectively functioning wing-coupling apparatus; the flight of these moths is very slow and feeble. In *Lampronia* the costal spines are still less spine-like, there are four rather strong frenulum spines, and a few elongate and longitudinally placed scales near the base of cubitus which may serve as a weak retinaculum for the frenulum spines. In Isocorypha the attachment of the female three-spined frenulum is subcostal; the retinaculum consists of the broad projecting scales from subcosta, and a tuft of stiff hair-like scales, occupying the same area as the hairs and scales clothing the male frenulum (Fig. 3, ♀). The female frenulum was observed to pass beneath these scales and hairs.

2. Prodoxidæ.

In *Prodoxus quinquepunctellus* the male subcostal retinaculum (Fig. 4) is an unspecialized broadly curved flat outgrowth from the costa, clothed with a series of stiff elongate scales which project beyond its free margin; the frenulum spine passes beneath this flap and lies against the wing between costa and subcosta. In *Tegeticula yuccasella* the frenulum-hook arises also from costa (Fig. 5), but is here of the usual form found throughout the Frenatæ, *i. e.*, its free end tapers and curls toward

the wing membrane, forming an effective catch for the frenulum spine. In *Prodoxus*, female, the costal spines retain their primitive hook-like character; in *Tegeticula* only the two proximal retain their spine-like character, but are straight, and are longer than any of the corresponding series in *Prodoxus;* they are long enough to reach beneath the projecting scales on costa of the fore wing, and may thus function as a frenulum before the true frenulum has reached a sufficient size to be functional. This condition suggests one possible mode of transition from functional costal spines to a functional single-spined frenulum with its specialized frenulum-hook; the subcostal retinaculum may originate first as a retinaculum for costal spines. A similar process of evolution of the function of the subcostal retinaculum was indicated in the female of certain species of *Nepticula*.

In *Prodoxus* the base of Cu_2 is apparently the effective holding structure for the costal spines; there is also the beginning of a subdorsal retinaculum. The scales in this position are longer than the general scale covering of the wing, and like it are almost longitudinally placed. Placed in this position they may serve as a catch for the costal spines, but would scarcely hold the more obliquely directed frenulum spines. As will be seen later the scales and hairs of the specialized subdorsal retinaculum, acting as a catch for the female frenulum spines, point toward costa.

3. Adelidæ.

The frenulum-hook in *Adela*, male, is similar to that of *Lampronia*. In the female the frenulum spines are rudimentary. The costal spines lie over a prominent part of the base of Cu_2 just beyond the cross-vein between Cu_2 and the first anal. It is possible that the tuft of bristles from the base of costa of the fore wing serves to hold the costal spines against the fore wing, as in this instance the costal spines are long enough to pass beneath this tuft. There is no subdorsal retinaculum in either sex.

4. Cossidæ.

In the Cossidæ, which some students (Turner, 1918, Tillyård, 1919b) regard as preserving the most primitive type of venation among existing Frenatæ, the male frenulum is sometimes rudimentary, or short and functionless; sometimes single-spined and caught by a frenulum-hook of the general type illustrated by Figure 6. The female frenulum is always rudimentary. In *Prionoxystus* a very different method of wing-coupling has developed; the underside of the inner margin of the fore wing hooks against a strong ridge along costa of the hind wing.

5. Tineidæ.

In this family it is possible to identify structures homologous with the costal spines, but in every instance, they have lost their holding function and with it, their characteristic structure.

The subcostal retinaculum in the male develops from subcosta or from the membrane immediately costalwards from it. It may be a flat outgrowth, densely clothed with scales, which curve down at its free

end (*Myrmecozela*). The chitinous catch itself may curve down at its free end, and be clothed with scales and long hairs (*Scardia*, *Monopis*, *Tinea*). The efficiency of this chitinous frenulum-hook is supplemented in *Myrmecozela* by a patch of closely set small scales lying under the frenulum-hook between radius and subcosta, and pointing obliquely toward subcosta.

The subdorsal retinaculum consists of long scales extending obliquely outward; it is more conspicuous in the male than in the female. The trend of evolution in the female is toward the development of a subcostal retinaculum, as shown in *Monopis*, *Myrmecozela*, and *Tinea*. In *Monopis* the scales of the subdorsal retinaculum form a continuous patch all the way to subcosta; this together with the dense projecting scaling from subcosta can easily function as a retinaculum for the frenulum spines. In *Myrmecozela*, female, the scales corresponding to the patch of close-set scales beneath the frenulum-hook in the male, are placed at right angles to radius, and do not lie flat against the wing; the female frenulum spines were observed to pass under these scales. In addition there are on subcosta, inwardly pointing, strongly chitinized linear scales, and scales covering these and overlapping the ends of the scales between radius and subcosta. In *Tinea* subcosta itself is swollen and clothed with dense projecting hairs and scales.

6. Acrolophidæ.

In *Acrolophus* the frenulum-hook is an outgrowth from the membrane between subcosta and costa, and its downwardly curved end is closely beset with very small scales. The frenulum lies on the costal side of subcosta. The subdorsal retinaculum consists of a tuft of longer scales and hairs and appears to be functional in the female.

7. Lyonetiidæ.

I have followed Meyrick in the broader definition of this family, including in it, *Tischeria*, *Coptotriche*, *Opostega*, *Coptodisca* and other genera sometimes placed elsewhere or given separate family rank. The family is chiefly remarkable for the conservation of some characters in primitive condition, together with a high degree of specialization of other characters. A striking example of this latter feature is the fact that the subcostal retinaculum of the female lags but little or not at all behind that of the male in degree of specialization.

In *Opostega* there is no functional frenulum in either sex and the wing-coupling apparatus in both sexes consists only of the series of costal spines and their retinacula. The fourteen or fifteen strongly curved costal spines lie close together, the whole forming a strong hook which catches onto a curve in the base of cubitus clothed with obliquely forward projecting scales into which the curved tips of the individual spines hook. In addition there is a slight overfolding of subcosta under which the costal spines slip when the wings are folded.

In many of the other genera of this family the modified costal spines may easily be differentiated from the rest of the scale covering of the hind wing as dark, more strongly chitinized but not curved

structures; they are not functional in any of these genera. In both male and female there is a functional frenulum, in the female usually made up of two closely associated spines.

In none of the genera observed (except *Opostega*) is there a functional subdorsal retinaculum, the few oblique scales in this position lie flat against the wing. Its function in the female is performed by a subcostal retinaculum of the same character as that of the male, and in the most specialized genera nearly or quite as specialized in structure as the male subcostal retinaculum.

The beginnings of a subcostal retinaculum are shown in both sexes as a thickening of subcosta, often a thickening of the entire costal area between costa and subcosta, with a tendency for subcosta to extend out over the wing, forming an elongate broadly rounded flat projection, scarcely more than the width of subcosta itself. The distal edge toward apex is clothed with specialized scales, sometimes narrow, sometimes broader and curved. Males are but little in advance of females. This is the general condition to be found in *Decadarchis*, *Eschatotype*, *Proleucoptera*, *Opogona*, in both sexes; in *Hieroxestis* a frenulum-hook of the usual form has been attained in the male. Supplementary holding structures in the way of larger or more elongate specialized scales inserted between radius and subcosta and directed obliquely toward the bulge in subcosta are often found.

In *Coptodisca* the chitinous projection from subcosta is in both sexes long, very broadly triangular, and bears on its distal free edge strongly chitinized linear scales, straight in the female, hooked in the male. The wing-coupling apparatus is thus typically Lyonetiid, and does not at all resemble that of the Heliozelidæ, where *Coptodisca* was formerly placed. In *Tischeria citrinipennella*, female, a row of curved scales fringes the enlarged projecting part of subcosta, forming a functional retinaculum. In the male a small, parallel-sided strongly curved flap growing out from the enlargement of subcosta constitutes a specialized chitinous frenulum-hook. A chitinous frenulum-hook of the type shown in Figure 6 occurs in both sexes in *Bucculatrix*.

8. Plutellidæ.

Throughout the family the subcostal retinaculum of the male is a chitinous outgrowth attached proximally to subcosta and beyond, to the membrane between costa and subcosta, and tapering to its curled free end. This type of frenulum-hook is illustrated by Figure 6.

The subdorsal retinaculum throughout the family presents a general unspecialized condition. It consists of a group of broad scales, distinguished principally by the fact that they are directed toward costa, and functions as a retinaculum for the three bristles of the female frenulum. In the male there is sometimes no differentiation of scales in this position.

9. Yponomeutidæ.

The frenulum-hook of the male in this family agrees in structure with that of the Plutellidæ. There is sometimes an attempt at a sub-

costal retinaculum in the female also, as for example in *Yponomeuta*, in which subcosta is swollen and at one place bears long narrow scales, which project inwardly almost at right angles to the vein.

The subdorsal retinaculum consists of a patch of scales projecting obliquely costalwards, broader and more closely placed in the female than in the male, and in the genera examined, with the possible exception of *Yponomeuta*, it is the only functional retinaculum in the female.

10. Gracilariidæ.

Throughout the family the subcostal retinaculum or frenulum-hook of the male is a slightly curved chitinous catch from subcosta, broad and little tapering in *Gracilaria*, narrower and more elongate in *Litho colletis*, and bearing at its end projecting curved scales. These scales in *Lithocolletis* sometimes curl under, forming a tube through which the frenulum spine passes. The only exception to this general type is found in *Apophthisis*, where the male subcostal retinaculum is of the same character as that of the female, described below.

The female subcostal retinaculum consists of a group of curved elongate scales attached to a swollen and bulging part of subcosta; in *Lithocolletis* these scales are fewer in number than in *Gracilaria*, and form a more highly specialized retinaculum. The scales of this specialized retinaculum are six or seven in number, regularly and closely placed, heavily chitinized and strongly hooked. In *Gracilaria* the subcostal is the only functional retinaculum for the two-spined female frenulum; in *Lithocolletis*, a group of long, conspicuously large scales constitutes a functional subdorsal retinaculum. A weak subdorsal retinaculum may be distinguished in the male *Lithocolletis*.

11. Scythridæ.

In Scythris the frenulum-hook of the male arises from a ridge extending outward in a line with the base of subcosta. The subcostal vein itself bends toward the middle of the wing beneath the frenulum-hook. This jog in the course of subcosta is of common occurrence in many families. Such a frenulum-hook is merely a slight modification of the type illustrated by Figure 6.

The subdorsal retinaculum varies in degree of specialization in different species; it sometimes functions alone as a retinaculum for the female frenulum; sometimes it acts in conjunction with a group of specialized scales projecting from subcosta. In the former case, it consists of a group of larger broader scales, which can catch the outer part of the frenulum spines. In the latter case (*Scythris impositella*), the scales of the subdorsal retinaculum are elongate, some attached within the cell, and meet a row of very narrow scales projecting inwardly from subcosta. An unspecialized subdorsal retinaculum is present in the male, the scales but little different from the general scale covering.

12. Epermeniidæ.

In Epermenia pimpinella the frenulum-hook originates as in *Scythris;* its sides are parallel. In *Idioglossa* the parallel-sided frenulum-hook is

long, much curved and covered with very long curved scales, some of them hair-like and extending about to the middle of the wing.

In *Epermenia* the subdorsal retinaculum of the male is a tuft of long scales; in the female the scales of this tuft are more elongate and reach nearly to subcosta.

A specialized retinaculum for the frenulum spines of the female is present in *Idioglossa*. It consists of a series of curved linear scales in a row within the cell and near to radius; over the ends of these project another series of very short, curved, and strongly chitinized linear scales attached to subcosta. No subdorsal retinaculum is present in the usual position in either sex in *Idioglossa*.

13. Elachistidæ.

No single form of retinaculum, either subcostal or subdorsal, is common to the entire family.

In *Elachista* the male frenulum-hook arises from subcosta and is of the usual type. In *Tinagma* its curl is diagonally, rather than longitudinally placed; this seems to be correlated with the position of the frenulum spine, which diverges sharply from the costal margin of the hind wing. In *Cælopæta* the frenulum-hook is of unsuual appearance; it is a dark opaque curled object, narrow and of equal width throughout, and seems to be the product of the fusion of a series of scales and their sockets side by side.

In *Elachista orestella* an unspecialized subdorsal retinaculum is present in both sexes; in *Elachista madarella* the scales of the subdorsal retinaculum are small, and in the female the chief holding structure is subcostal. This retinaculum consists of long bristles extending inward from subcosta and lying close to the wing, covered by long scales. In *Tinagma* the subdorsal retinaculum consists merely of a few scales, and here again in the female the functional retinaculum is subcostal consisting of a row of curved broad scales along subcosta. In *Cælopæta* the subdorsal retinaculum in the female consists of a tuft of curved scales; a more efficient subcostal retinaculum is present, consisting of a row of about ten strong narrow hooked scales, into which the four strong spines of the female frenulum may easily catch. The frenulum-hook of the male arises apparently through approximation and fusion of these scales.

14. Coleophoridæ.

The male subcostal retinaculum is the usual frenulum-hook, and arises from the subcostal vein.

In most species of *Coleophora*, the female frenulum consists of one heavy bristle, weaker however than the male frenulum spine, and a second weak and functionless bristle, about half the length of the heavier bristle. A highly specialized subcostal retinaculum serves as a catch for this specialized female frenulum. This retinaculum consists of two parts; a series of closely set curved scales along a swollen and projecting part of subcosta, which taken together sometimes form a retinaculum in outline resembling the male frenulum-hook; a row of elongate, raised,

slightly curved scales attached to the wing membrane just dorsad of subcosta and directed obliquely toward subcosta. These two series of scales together form a tube through which the frenulum passes. There is no subdorsal retinaculum.

15. Glyphipterygidæ.

In the male the frenulum-hook is a triangular chitinous flap from a thickened subcostal vein, and curving toward the wing at its apex.

In the females a tuft of rather stiff long hairs projects from the thickened and slightly overfolded subcostal vein. The two frenulum spines pass beneath these and lie in the faint groove formed by the overfolding subcosta.

There is no subdorsal retinaculum in either sex.

16. Heliozelidæ.

In both *Heliozela* and *Antispila*, the male frenulum spine passes beneath a long narrow costal fold beginning almost at the base of the wing and broadening to overlap subcosta near base, thence gradually narrowing. The female frenulum consists of three or four short heavy spines which merely lie in the concave under surface of the fore wing, with no apparent holding structure.

17. Heliodinidæ.

The retinaculum is subcostal in both sexes, in the genera examined, except in *Erineda*, where in the female it is a combined subcostal and subdorsal retinaculum. In *Lithariapteryx* the retinaculum is identical in structure in both sexes.

The subcostal retinaculum in the male is a swelling and slight overfolding of subcosta edged with curved scales (*Lithariapteryx);* a short, broad, and but little curved frenulum-hook running out in a long ridge along subcosta beyond the usual ending of the frenulum-hook (*Erineda);* a curved chitinous hook (*Heliodines*); or a chitinous hook with its free end recurved to form a cylindrical tube (*Schreckensteinia*).

In *Lithariapteryx*, *Heliodines* and *Schreckensteinia*, a swollen and slightly overfolding subcosta, edged with curved scales forms the retinaculum in the female; the frenulum in *Heliodines* is made up of one heavy and one fine bristle, as in *Coleophora;* in *Lithariapteryx* and *Schreckensteinia* of three closely associated bristles. In *Erineda* the retinaculum in the female (Fig. 9) is made up of three series of setæ; sixteen or twenty short setæ pointing obliquely inward from a swelling of subcosta, a second more widely separated set inserted near the base of radius and pointing obliquely outward toward subcosta, a third set of long setæ on cubitus, extending over and beyond those on radius.

18. Aegeriidæ.

A single-spined frenulum has been attained in both males and females in this family, and is caught under an overfold of subcosta projecting and approaching close to the wing membrane at one point. This frenulum-hook shows some resemblance to that of *Erineda* in the

allied family Heliodinidæ. There is also a row of scales pointing costalwards from radius, which aids in holding the frenulum more securely in place.

In addition, the dorsal margin of the fore wing is rolled under and catches firmly nearly the whole length of the costal margin of the hind wing, which is similarly rolled over.

19. Eucosmidæ, Tortricidæ, Phalonidæ.

There is in the Tortricid group a tendency toward transfer of the female frenulum from a subdorsal to a subcostal retinaculum. Thus in *Argyroploce constellatana* and *Eucosma otiosana* (Eucosmidæ), the subdorsal retinaculum for the female frenulum of three nearly equal spines consists of a tuft of spreading, elongate or hair-like scales, and it alone is functional. *Peronea* (Tortricidæ) agrees with Eucosmidæ, but in *Cacœcia rosaceana* (Tortricidæ), the scales of the subdorsal retinaculum are comparatively short and the spines do not hold well in it; one of the frenulum spines is heavier than the other two and may pass beneath the elongate scales fringing a swollen part of subcosta. In *Phalonia floccosana* there is in addition to the large tuft of elongate scales forming the subdorsal retinaculum, an at least partially functional subcostal retinaculum. In the mounted specimens examined, the two rather heavy frenulum spines lie beneath a series of very long scales from subcosta, the underneath ones linear, and strongly chitinized. These overlap the scales of the subdorsal retinaculum.

In all cases the subdorsal retinaculum of the male is less specialized than that of the female and the scales are often closely appressed to the wing membrane.

The subcostal retinaculum—frenulum-hook—of the male is comparatively small, variable in shape, usually but little curved, and may arise as shown in Figure 6 or from subcosta alone.

20. Ethmiidæ.

In *Ethmia* and in *Eumeyrickia*, the frenulum-hook of the male is the usual curved chitinous flap of the type illustrated in Figure 6. The subdorsal retinaculum is alone functional in the female; it consists of a group of broad, somewhat raised scales.

21. Stenomidæ.

In origin from the wing, the frenulum-hook of the male is of the type illustrated in Figure 6; it is in this family characteristically broad, low, closely appressed to the wing and very slightly curved. In *Stenoma humilis* and *S. algidella*, it starts from a subcosta much thickened at base and is a broad chitinous tapering flap, its free side toward base convex, its outer side concave. In *S. mistrella* the frenulum-hook is much like that of *Menesta*. In *Menesta* the frenulum-hook is an almost semicircular flap, only slightly curved down, and edged, at half way around it, with small curved scales.

The subdorsal retinaculum functions in the female. It consists in this sex of a tuft of very long, hair-like scales projecting across the cell.

A dense bunch (*Stenoma*) or a row (*Menesta*) of short linear scales projects from subcosta and almost meets the subdorsal retinaculum. In the male, the scales of the subdorsal retinaculum are elongate, but not hair-like (*Stenoma*). In *Menesta* there is no differentiation of scales in this position in the male.

Setiostoma, formerly included in Glyphipterygidæ, was transferred by Busck on genitalic characters to Stenomidæ, where the type of wing-coupling apparatus also places it.

22. Oecophoridæ.

The frenulum-hook of the male, with slight variation in shape and amount of curling, is of the same character throughout the family; in general it agrees with Figure 6. Subcosta curves toward the middle of the wing beneath the frenulum-hook and is somewhat less prominent there than elsewhere.

The female frenulum is two- or three-spined and catches into a subdorsal retinaculum, which is neither very conspicuous nor very highly specialized. In *Psilocorsis* the scales are rather broad and closely set; in *Depressaria* there are some hair-like scales at the proximal end of the patch. In the latter there are also some curved scales from subcosta, suggesting the beginning of a subcostal retinaculum. There is an unspecialized and non-functioning subdorsal retinaculum also in the male.

23. Blastobasidæ.

The general structure of the wing-coupling apparatus is uniform throughout the family and is characteristic for the family in the female. The following description is made from the examination of *Valentinia glandulella*.

The retinaculum for the frenulum spines of the female consists of a patch of scales, some, the longest, in the position of the subdorsal retinaculum; the patch extends diagonally across the cell and continues (toward apex) as a row of short, rather elongate scales dorsad to radius. There is here then both a subdorsal retinaculum which seems to be the main functional one, and a subradial one, into which only the extreme tips of the frenulum spines could catch.

The subdorsal retinaculum is preserved in the male, but does not function. There are also a few scales projecting forward from the inner side of radius, but there is no such specialization as is seen in the female.

The subcostal retinaculum in the male is a chitinous hook of the type illustrated by Figure 6.

24. Gelechiidæ.

Throughout the family the subcostal retinaculum in the male is a curved chitinous frenulum-hook, of the type shown in Figure 6, and very similar to the frenulum-hook in the Oecophoridæ.

There is no indication of a subdorsal retinaculum in either sex anywhere in the family; its function in the female is performed by a highly specialized retinaculum, which may be termed subradial. The

subradial retinaculum, which is apparently a recognition character for the family, consists of a row of linear, strongly chitinized scales, either straight or curved, attached to the wing membrane in the cell just dorsad of radius and pointing toward costa (Fig. 7). This row of scales engages the three equal frenulum spines. The subradial retinaculum is distad of the position of the subdorsal retinaculum. There is also a row of elongate scales, usually curved, projecting inwardly from subcosta, and sometimes almost meeting the scales of the subradial retinaculum. These scales may supplement the subradial retinaculum in flight.

A comparison of the female retinaculum in Gelechiidæ and Blastobasidæ suggests the very interesting possibility that a course of development involving a gradual replacement in function of the subdorsal retinaculum by a subradial retinaculum, concomitant with a lengthening and strengthening of the frenulum spines, and subsequent loss of the subdorsal retinaculum, may have brought about the condition observed in the Gelechiidæ.

25. Cosmopterygidæ.

This family shows a transition in the female from a functional subdorsal retinaculum alone, through a functional subdorsal and subcostal retinaculum working together, with a correlated division of frenulum spines, to a functional subcostal retinaculum alone.

In *Lymnœcia phragmitella* the three frenulum spines are of equal length and stoutness and are held by a subdorsal retinaculum consisting of a tuft of elongate scales. In *Mompha stellella* (Fig. 8) two of the frenulum spines are longer and stouter than those in *Lymnœcia*, and are caught by a subcostal retinaculum consisting of a row of curved strongly chitinized, linear, almost bristle-like scales inserted on subcosta. The third frenulum spine is much shorter and weak and diverges from the other two; it alone catches into a subdorsal retinaculum consisting of a tuft of elongate scales. In *Cosmopteryx clemensella* there are but two frenulum spines and these are caught in a subcostal retinaculum consisting of a row of closely placed, curved, hair-like scales from subcosta, and a row of scales from the membrane between radius and subcosta, pointing toward them. There is no subdorsal retinaculum in *Cosmopteryx* even in the female.

The subcostal retinaculum in the male is a chitinous hook from the subcostal vein, sometimes parallel-sided (*Cosmopteryx*), sometimes more or less triangular (*Mompha*). A subdorsal retinaculum consisting of a patch of small scales is sometimes present (*Mompha*).

26. Megalopygidæ.

In *Lagoa crispata* a subdorsal retinaculum only is functional in both sexes. The male frenulum spine is short and merely catches into the dense scaling and hairs in the position of the subdorsal retinaculum, a condition in the male more primitive than that observed in any other Frenatæ except the Cossidæ and *Opostega*. The female frenulum is a tuft of soft bristles.

27. Limacodidæ.

In the males the single-spined frenulum catches into a chitinous frenulum-hook from subcosta. The subdorsal retinaculum is either absent, or the scales are scarcely different from the rest of the scale covering.

In the females a subdorsal retinaculum is functional. In *Parasa chloris* there is a dense clothing of long hairs near the base of the underside of the fore wings, the most dorsally placed group of these being in the position of the subdorsal retinaculum, and probably engaging the numerous fine bristles of the frenulum. In *Tortricidia testacea* the frenulum spines are fewer in number and longer and catch into a subdorsal retinaculum of scales of the character found in other families.

28. Psychidæ.

In this family the frenulum-hook of the male arises from the membrane between the costa and the subcostal vein, and may be parallel-sided and much curled (*Thyridopteryx*), or broadly triangular and flat (*Solenobia*). There is no subdorsal retinaculum.

29. Zygænidæ.

In this family, the male frenulum-hook is of the type shown in Figure 6. The subdorsal retinaculum when present at all in the male consists of a few closely appressed scales. The subdorsal retinaculum in the female is weak and inefficient; in *Malthaca dimidiata* it consists of a bunch of long scales; in *Harrisina americana* of merely a few scales projecting over Cu_1.

30. Thyridæ.

In this family there is a chitinous frenulum-hook from subcosta in the male, also a subdorsal retinaculum. The scales forming the subdorsal retinaculum are elongate and thus easily differentiated from the heavy covering of broad loose scales which clothe the underside of the wing; in the female the scales of the subdorsal retinaculum extend over a greater length of wing than in the male.

31. Pyralidæ.

The frenulum-hook of the male is a long, narrow, curved chitinous bar from subcosta, reaching so far over the wing that the frenulum spine hooks onto it, and beyond it, the tip of the frenulum spine catches into the well developed tuft of scales forming the subdorsal retinaculum. Sometimes the curved end of the frenulum-hook reaches beyond Cu_1, and lies alongside of the subdorsal retinaculum, and the two function together as a double catch for the frenulum spine; a peculiar specialization not observed elsewhere. The subdorsal retinaculum is about equally well developed in both sexes; it is alone functional in the female.

32. Other Families.

It is not the purpose of this paper to discuss the higher families of the frenulum conservers; a summary by Tillyard (1919b, Appendix B)

of the work of other observers shows that no specializations not present in the lower families have been acquired; there is sometimes a loss of the frenulun-hook in the male. It may be stated in general, however, that both subcostal and subdorsal retinacula are present in the male, the former functional; a subdorsal retinaculum is present and functional in the female, with an occasional attempt at a subcostal retinaculum.

III. General Summary of the Types of Retinacula.

a. Subdorsal Retinaculum.

The term subdorsal retinaculum is used to refer to the group of more or less specialized scales, commonly present in both sexes and occupying a position between the bases of Cu_1 and Cu_2 respectively, occasionally encroaching on Cu_1 itself and rarely extending into the cell toward radius (Blastobasidæ) and sometimes beyond to subcosta (Tineidæ). It may consist of a few scales placed longitudinally or nearly so (*Prodoxus*, *Lampronia*, *Opostega*) and not differing greatly from the rest of the wing covering. In all except the most primitive groups, the scales of the subdorsal retinaculum are in general directed toward costa. These scales may be broad (Plutellidæ, Yponomeutidæ, Ethmiidæ, some Oecophoridæ) and somewhat raised above the wing surface, or may be elongate, sometimes hair-like, forming a dense tuft (Tineidæ, Acrolophidæ, Gracilariidæ, Tortricina, Stenomidæ, some Oecophoridæ, Cosmopterygidæ, Megalopygidæ and others); the last is the most specialized and commonest form in the Frenatæ, especially in the higher families. Where the subdorsal retinaculum has lost its function in the female, the scales in this position may be few and small (Lyonetiidæ and some Elachistidæ). On the other hand in many families, though not functional in the male, the subdorsal retinaculum is retained in a condition nearly or quite as specialized as in the female. In the Nepticulidæ, the scales of the subdorsal retinaculum are arranged in regular rows.

The subdorsal retinaculum is a catch for the costal spines (*Prodoxus*, *Opostega*, Nepticulidæ), the frenulum spines of the female, rarely for the single-spined frenulum of the male (*Lagoa*); in some male Pyralids, both the frenulum-hook and the subdorsal retinaculum catch the frenulum. Its efficiency may be added to by scales pointing toward it from subcosta. There thus results a combination subcostal and subdorsal retinaculum (*Monopis*, *Scythris*, *Phalonia*, *Stenomidæ*). The subdorsal may catch but one of the female frenulum spines, the others being caught in a subcostal retinaculum (some Cosmopterygidæ).

The subdorsal retinaculum is present in the males in many families, usually in less specialized condition than in the female, but is rarely functional. It is sometimes entirely absent (Micropterygidæ, Incurvariidæ, Adelidæ, Lyonetiidæ, Coleophoridæ, Gelechiidæ and many other families). In these cases the base of Cu may act as a holding structure for costal spines (Micropterygidæ, some Incurvariidæ, Adelidæ); there may be no efficient holding structure for the female frenulum spines (*Greya*, Heliozelidæ, Glyphipterygidæ); or its function in the female may be performed by other specialized retinacula.

b. Subcostal Retinaculum.

1. Frenulum-hook.

The frenulum-hook is a chitinous double-walled outgrowth from the wing. It may arise from the costa (Prodoxidæ, some Incurvariidæ, Heliozelidæ), from the wing membrane between costa and subcosta (*Chalceopla*, Psychidæ, Acrolophidæ), from the subcostal vein (Tineidæ, Lyonetiidæ, Glyphipterygidæ, Gracilariidæ, Elachistidæ, Heliodinidæ, Coleophoridæ, some Tortricina, Aegeriidæ, Cosmopterygidæ, Limacodidæ and other families), or from a ridge extending from subcosta obliquely across the wing toward the costa (Fig. 6). These last two types are closely related and probably homologous. The frenulum-hook illustrated by Figure 6 is found in some Incurvariidæ, in Adelidæ, Plutellidæ, Yponomeutidæ, Scythridæ, Epermeniidæ, some Tortricina, Stenomidæ, Oecophoridæ, Gelechiidæ, Zygænidæ.

The frenulum-hook varies in shape; it may be attached as much as one-fourth the wing length and be thus a long fold or a broad triangle; it may be a short outgrowth scarcely more than the width of the subcostal vein; nearly semicircular, with evenly rounded free margin; triangular, rather abruptly tapering, with its truncate free end curled under toward the wing margin and forming an effective hook; or a narrow, parallel-sided curved bar. Where the free end of the frenulum-hook is but little curled or where the outgrowth is but little more than a bulging of subcosta, the hook-like character may be attained by a fringing of curved scales. A dense covering of scales conceals the frenulum-hook.

The frenulum-hook as above described is a character in general confined to the male. Rarely the female attains or approaches this specialized structure (Aegeriidæ, some Lyonetiidæ). The beginnings of its development are often indicated in the female. In addition to the fringing of the free end with curved scales, sometimes long (*Idioglossa*), other accessory specializations, which may add to its efficiency, are often found upon the wing in the region of the frenulum-hook. A patch of small scales points toward costa beneath the frenulum-hook in some Tineidæ; a patch of larger or more elongate scales between radius and subcosta points toward the bulge in subcosta in Lyonetiidæ.

In a few males there is no subcostal retinaculum (Micropterygidæ, *Opostega*, some Cossidæ, Megalopygidæ).

2. Other forms of subcostal retinacula.

MALE.—Instead of the more or less well developed chitinous frenulum-hook present in most males, there are sometimes in the male subcostal retinacula of other types. Thus in most male Nepticulidæ, the subcostal retinaculum consists of a parallel-placed series of looped, linear, heavily chitinized scales inserted on subcosta. In *Cælopœta* (Elachistidæ) the frenulum-hook appears to be the product of the fusion side by side of a series of curved scales. In many genera of Lyonetiidæ the male subcostal retinaculum has not yet attained the status of a frenulum-hook.

FEMALE.—Subcostal retinacula in the female vary all the way from scarcely more than the usual heavy scaling over the base of subcosta (*Isocorypha*, some Tineidæ, Scythridæ, Phalonidæ) under which the frenulum spines merely lie, to structures as efficient as the usual frenulum-hook of the male. With advance in specialization, the scales forming the subcostal retinaculum are found to be attached to a definitely limited part of subcosta, and to be of specialized form. Thus they may be straight or curved, sometimes broad, sometimes linear, even bristle-like (a few Nepticulidæ, *Tinea*, Lyonetiidæ, *Yponomeuta*, Elachistidæ, *Coleophora*, Glyphipterygidæ, Heliodinidæ, Gracilariidæ and others). Very often the subcosta at this place is swollen and even slightly overfolded, indicating the initiation of development of the chitinous frenulum-hook. In the Lyonetiidæ this type of subcostal retinaculum in the female has reached a stage of development where it can be considered a primitive frenulum-hook and is thus treated.

The scales of the subcostal retinaculum of the female sometimes form a hook as efficient as the chitinous frenulum-hook of the male, particularly when other groups of scales, such as those described below, add to the security with which the frenulum spines are held. In *Lithocolletis*, six or seven heavily chitinized, hooked scales, closely placed, form a catch for the frenulum; a similar row of hooked scales is present in *Cælopœta;* the closely set curved scales of *Coleophora* present in outline a structure resembling the male frenulum-hook.

Accessory groups of scales, supplementing the holding function of the subcostal retinaculum in the female, when in the same position as homologous scales in the males of the same species, are usually more specialized in structure and direction. Thus in *Myrmecozela* the scales between radius and subcosta, homologous with the small scales beneath the frenulum-hook of the male, are at right angles to radius and raised in the female. In *Cosmopteryx* a row of scales from the membrane between radius and subcosta points toward the subcostal series. In *Coleophora* a series of raised, curved scales attached just dorsad of subcosta, forms with the subcostal series a tube through which the frenulum passes.

In *Mompha* and some other genera of the Cosmopterygidæ there is a division of the female frenulum spines, two spines caught by a row of linear curved subcostal scales, the third caught by the subdorsal retinaculum.

c. Unusual and Characteristic Types of Retinacula.

A few exceptional retinacula, which are in some cases characteristic of and confined to certain families, remain to be mentioned.

In *Erineda* the female retinaculum consists of three series of setæ, subcostal, radial and cubital respectively; the first directed toward dorsum, the other two series toward costa.

In *Idioglossa*, female, in addition to the curved linear scales on subcosta, there is a subradial series just within the cell.

In the females in the Blastobasidæ and the Gelechiidæ there is a subradial retinaculum, a type which, with the exception only of *Idio-*

glossa, is confined to these two families and in the Gelechiidæ effectively functions alone. In the Blastobastidæ the subradial retinaculum is continuous with the subdorsal retinaculum and consists of a row of short scales in the cell dorsad to radius. In the Gelechiidæ the subdorsal retinaculum is entirely absent, and the subradial retinaculum is a highly specialized row of linear, strongly chitinized scales, either straight or curved.

IV. Phylogenetic Development of the Frenulum and Its Retinaculum.

The frenulum, as is well known, is a development of the weak unspecialized group of bristles or setæ borne on the costal sclerite of the hind wing. Except in the Micropterygidæ and Hepialidæ, and in *Opostega* and a few Cossidæ only in the Frenatæ, the male frenulum is a single spine formed by the fusion of several bristles. The female frenulum in many of the most primitive Lepidoptera (Micropterygidæ, Nepticulidæ, Incurvariidæ, Prodoxidæ, Adelidæ) consists of bristles so weak and short as to be useless in wing-coupling. Where functional, it usually consists of several bristles, often three or two; in *Coleophora* and in *Heliodines*, of one heavy functional bristle, and one weak useless bristle, i. e., there is a degeneration and disappearance of the extra bristle, instead of a fusion; in Aegeriidæ, the female frenulum is also a single spine. The frenulum is thus an homologous structure throughout the Lepidoptera; its variations are all part of the same developmental series.

In some cases at least, the development of a single-spined frenulum antedates the development of a subcostal retinaculum (*Lagoa*, some Cossidæ); but in most cases the attainment of a single-spined frenulum is coincident with the development of some sort of a subcostal retinaculum which functions effectively. The whole process of development of the frenulum, beginning with the gradual lengthening and strengthening of the minute bristles constituting the primitive frenulum, and the lessening in number through fusion or atrophy, must have been orthogenetic, and the initiation of the process must have taken place in the common ancestry of the Frenatæ and the Nepticulidæ. Stages in the development from minute bristles to a functional frenulum in the female may be observed within the confines of a single family (Incurvariidæ) and it is also probable that the actual culmination of the process in the male, resulting in the very strong and specialized single spine, may have occurred independently in several other groups, just as it has in the Cossidæ; to this extent we must postulate convergence in development.

The retinacula for the frenulum spines do not exhibit the same degree of uniformity and homology as the frenulum itself. Preceding the phylogenetic development of a functional frenulum, a similar role in wing-coupling was performed by the costal spines. A study of their manner of engaging the fore wing and of the structures which develop on the fore wing in connection with this function, throws some light

upon the origin and development of the retinacula for the frenulum spines. The indications point to the conclusion that phylogenetically the retinacula for the frenulum had their beginnings as retinacula for the costal spines, and that with the loss of function of the costal spines, their retinacula became the retinacula for the frenulum, which had gradually developed to a sufficient length to be functional.

The earliest retinaculum for the costal spines is merely the prominent base of cubitus, usually Cu_2, or sometimes Cu_1; as shown in *Mnemonica*, *Chalceopla*, *Adela*. Later a few scales of different size than the general wing covering, but still longitudinally placed, may be distinguished just costalwards of Cu_2 (*Prodoxus*); these form a firmer attachment for the costal spines than the base of Cu_2 alone. In Nepticulidæ rows of linear scales near Cu_2 engage the costal spines. Longitudinal scales of the form found in *Prodoxus* are retained in *Lampronia*, where their function is to hold the weak frenulum spines of the female rather than the costal spines, which have lost their holding function. The subdorsal retinaculum is here then for the first time acting as a retinaculum for the frenulum spines. In other words the subdorsal retinaculum arises in phylogeny first as a retinaculum for the costal spines, and later with the attainment of functional size by the female frenulum, becomes its retinaculum; its scales are at first longitudinally placed and are sufficiently effective in holding the more transversely directed costal spines, but inefficient as holding structures for the more longitudinally directed frenulum. In all higher groups the scales of the subdorsal retinaculum may be differentiated by direction as well as by structure; they point obliquely or almost directly toward costa, and have the highly specialized character described previously under the heading of subdorsal retinaculum.

With the taking over of the function of the subdorsal retinaculum in the female by other specialized structures as retinacula, it tends to disappear, so that its absence may be due to loss in the more specialized forms. It is generally, in these instances, absent in both sexes, as in Coleophoridæ, Glyphipterygidæ, most Heliodinidæ, some Cosmopterygidæ, *Idioglossa*, *Gracilaria;* or merely vestigial, as in some Lyonetiidæ and some male Cosmopterygidæ. In the Tineidæ, where the trend of evolution is toward a subcostal retinaculum in the female, we have the phenomenon of a more highly developed subdorsal retinaculum (though non-functioning) in the male than in the female; it is apparently in the male a persistent character handed down unchanged.

The development of a subcostal retinaculum in the female and the actual transfer of the female frenulum from a subdorsal to a subcostal or other retinaculum seems to be correlated, as far as observations go, with a lengthening and strengthening of some or all of the bristles, with sometimes a gradual loss of one or more bristles. The subcostal retinaculum in the female has its beginnings in more or less specialized scales which develop on the area of contact between the fore wing and the lengthened frenulum bristles, that is on subcosta or on the membrane between subcosta and radius, or over the entire area between subcosta and the subdorsal retinaculum. In intermediate forms both subcostal

and subdorsal retinaculum are retained (Tineidæ, Phalonidæ, Gracilariidæ, Scythridæ, Elachistidæ, some Cosmopterygidæ), one supplementing the other. The stages in the transfer from a subdorsal to a subcostal retinaculum in the female are preserved in the Cosmopterygidæ and have been described under that family. From the evidence given by the Blastobasidæ, the sub-radial retinaculum, present in that family and in Gelechiidæ and in *Idioglossa*, arises as an extension of the subdorsal retinaculum, directly correlated with the lengthening and strengthening of the frenulum spines.

From the close agreement in form between the male and female subcostal retinaculum in some families, notably in the Lyonetiidæ, it is highly probably that the origin of the subcostal retinaculum in the male can be explained in the manner which has just been outlined for the female, but the specialization has gone a step farther and has involved the wing membrane.

Other evidence seems to suggest that in some instances the subcostal retinaculum originated first as a retinaculum for at least some, perhaps only the most proximal of the costal spines. It was observed that in *Tegeticula*, female, the two proximal of the costal spines alone retain their spine-like character and are longer than any of the corresponding series in *Prodoxus*, the nearest allied genus; they are long enough to reach beneath the projecting scales from the costa of the fore wing, and may thus function in the same way as the frenulum. A parallel case is observed in the Nepticulidæ, where in a few specialized females, there is the beginning of a subcostal retinaculum, similar to that of the male, which may catch the unusually long costal spines. The costal spines may thus function as a frenulum up to the time the frenulum reaches a sufficient size to take over the holding function. The subcostal retinaculum, already in existence as a retinaculum for the costal spines, then becomes the retinaculum for the frenulum. It is interesting to note, but may be without significance, that in Prodoxidæ and most Incurvariidæ, the male subcostal retinaculum has its origin from costa or the membrane between costa and subcosta, an unusual position, shared by but few other groups.

The fact that the chitinous frenulum-hook is not constant in place of origin from the wing and hence that the different types of frenulum-hook (except the two arising from the subcostal vein) can be derived neither from one another nor from any single type, suggests that this form of subcostal retinaculum must have originated many times in the phylogeny of the Lepidoptera. Closely related families, sometimes derived one from the other, may exhibit the two subcostal types. If present family limits are to be maintained, we must even conclude that the frenulum-hook has arisen more than once within the same family; thus in the Incurvariidæ, it develops from costa, from the membrane between costa and subcosta or is attached to subcosta and to the membrane. As the Incurvariidæ constitute one of the most primitive families of the Frenatæ, it might be supposed that the frenulum-hook originated after the isolation of these primitive forms in the many branched frenate line.

V. Application to Phylogeny and Classification of the Lepidoptera.

It may be stated as a general principle that it is unsafe to base phylogenetic conclusions on any single character, however valuable that character may seem to be in determining relationships. It is the sum of all the characters which must be considered, but each individual character plays its part in corroborating or contradicting the testimony of other characters.

The Nepticulidæ, in which the females preserve costal spines and sometimes also a functional fibula, is a group divergent from the other Lepidoptera.

In the Frenatæ those groups which conserve at least in the female, the primitive mode of wing-coupling by means of costal spines, may of course be considered the most primitive groups. The great variation in the place of origin of the male frenulum-hook in the three families with functional costal spines, Prodoxidæ, Incurvariidæ and Adelidæ, suggests their very early separation from the frenate stem. In all other families, except the Psychidæ, Acrolophidæ and Heliozelidæ, the frenulum-hook is of constant subcostal origin

Again, the comparatively primitive condition of the male frenulum in some Cossidæ and in Megalopygidæ places them and their known allies low in the scale.

When we come to the remaining groups of the so-called Microlepidoptera, we find that the frenulum and its retinaculum offer no evidence of the manner of branching of the phylogenetic stem, and very little evidence upon which to base a grouping of allied families. This is in part due to the uniformity of the male frenulum and its frenulum-hook, and in part to the fact that although the general tendency in the female is toward the replacement of the subdorsal retinaculum by other retinacula, the results are sometimes so different in groups known to be related, and on the other hand, sometimes so similar in unrelated groups that they are altogether unreliable as criteria of relationships.

A few generalizations may be made. In the Tineidæ and Lyonetiidæ, the general trend of evolution toward a subcostal retinaculum in both sexes even in the most primitive members of these families, and the similar scaling between subcosta and radius, confirm their relationship determined from other characters. The Yponomeutid and Plutellid line shows no such early tendency toward the development of a subcostal retinaculum in the female, although the specialized members of many of the families in this line of descent, have attained a subcostal retinaculum in the female. One group of families, comprising the Cosmopterygidæ, Gelechiidæ, Blastobasidæ, Stenomidæ and Oecophoridæ, lags behind in the loss of the subdorsal retinaculum, but some of its members have acquired distinctive and unique specializations. Thus the subradial retinaculum in the female is a family characteristic in the Gelechiidæ; in the Blastobasidæ both subdorsal and subradial retinacula are found.

Occasionally the character of the wing-coupling apparatus may aid in deciding the affinities of a form where the evidence afforded by other characters is conflicting. Thus, *Menesta*, placed in Stenomidæ by general wing structure and pupal characters, and in Gelechiidæ by its male genitalia, is Stenomid in wing-coupling, and does not exhibit the diagnostic Gelechiid subradial retinaculum. The position of *Setiostoma* in the Stenomidæ, taken out of the Glyphipterygidæ by Busck on the basis of genitalic characters, is confirmed by wing-coupling characters. *Coptodisca* does not resemble the Heliozelidæ in the character of its frenulum and retinaculum in either sex, but is typically Lyonetiid.

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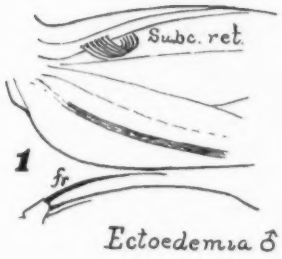
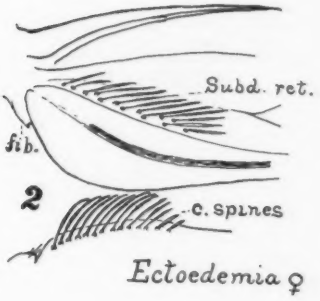
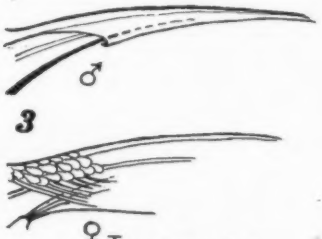
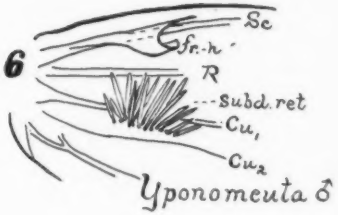
EXPLANATION OF PLATE XXIII.

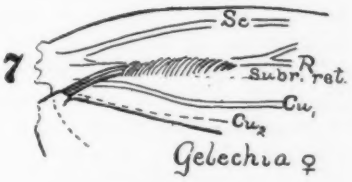
1. *Ectædemia heinrichi*, male; subcostal retinaculum (subc. ret.) and single-spined frenulum (fr.).
2. *Ectædemia heinrichi*, female; subdorsal retinaculum (subd. ret.), fibula (fib.); costal spines (c. spines) on upper side of hind wing.
3. Subcostal retinaculum in male and in female, *Isocorypha mediostriatella*.
4. Frenulum-hook (fr. h.), *Prodoxus quinquepunctellus*, male.
5. Frenulum-hook (fr. h.), *Tegiticula yuccasella*, male.
6. Frenulum-hook (fr. h.) and subdorsal retinaculum (subd. ret.), *Yponomeuta multipunctella*, male.
7. Subradial retinaculum (subr. ret.), *Gelechia cercerisella*, female.
8. Wing-coupling apparatus of *Mompha stellella*, female.
9. Retinaculum for frenulum spines, *Erineda ænea*, female.

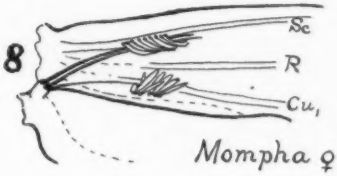


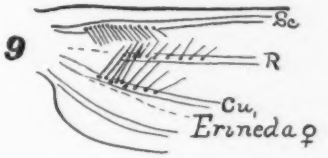












Annette F. Braun

ON THE NATURE OF THE COLOR PATTERNS IN HETEROPTERA WITH DATA ON THE EFFECTS PRODUCED BY TEMPERATURE AND HUMIDITY.*

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Recently there has appeared in the 19th Report of the Minnesota State Entomologist, my account of the life history and biology of *Perillus bioculatus*, a species of stink-bug that proves to be an excellent starting point for a study on the nature of color in Hemiptera. To give a proper setting for the present paper I would like to review briefly my work with this insect, or that part having a bearing on the nature of color in Heteroptera.

My attention was first directed to *Perillus bioculatus* when specimens were found feeding upon the Colorado potato beetle during July, 1913, in Genesee County, New York. Upon finding a red and black bug (Plate XXIV, Fig. 15) mating with a white and black individual (Plate XXIV, Fig. 1), the idea immediately occurred that here was a fine opportunity to study color inheritance in an insect. Studies were immediately begun, and more or less time has been given each year since to the rearing of this Pentatomid, except for the years 1917 and 1918. After the close of the war and with my removal to Minnesota in 1919, the study of Perillus was begun anew when the species was found fairly abundant in the vicinity of St. Paul. The first three years, or from 1913 to 1915, inclusive, were given over to breeding work and the study of color inheritance in the bugs. By the close of 1915 it became quite evident that the color forms could not be segregated by ordinary methods of breeding, but that individual colors were more dependent on the external conditions under which the bugs were reared. The season of 1916 was given over to a study of the factors influencing the color pattern of the bugs. The work on Perillus at Minnesota during the past four years has been

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chiefly on the nature of color, as well as a continuation of study on the factors affecting the color of individual bugs.

The color varieties of *Perillus bioculatus* fall largely within three color pattern limits, although in a large series of specimens extreme forms (Plate XXIV, Figs. 16-21) may be found, as well as intergrades which connect the three common color forms. These latter varieties are: (1) The white color form (Plate XXIV, Fig. 1); (2) yellow color form (Plate XXIV, Figs. 11-12); (3) red color form (Plate XXIV, Figs. 14-15). It was the mating of red and black forms with the white and black forms which first aroused my interest, namely, what would the progeny be? Apparently, here was a problem in breeding color varieties of an insect which offered an opportunity of comparing inheritance of animal colors with the well known work of Mendel on sweet peas.

After three seasons of breeding work trying to establish pure lines of the white color form, and of a red color form, it became perfectly clear that the color pattern of individual bugs was influenced more by external conditions rather than by characters inherited from the parents. My records show that during this period 68 pairs of *Perillus bioculatus* were used in the breeding experiments. Eventually, all the progeny of the white parents became yellow or red forms, this occurring in the fall generation or in the spring. The progeny of red parents all became yellow or white during the hot weeks of July or August, and thus the parent type could not be maintained. Again in 1921, an effort was made to breed for a pure line of white color forms, but all the progeny from three pairs of white bugs became either yellow or red during the second or early fall generation. On a few occasions, extreme dark color forms such as are shown in Figures 19 and 20 (Plate XXIV) were bred with the hope that some unusual variety might be segregated, but the progeny of all such forms developed into ordinary yellow and black, or white and black individuals, under summer temperatures (80° to 90° F.) as maintained in the laboratory.

Having seen the various color forms that appear in *Perillus bioculatus*, we will turn to a physical examination of the color pattern. The principal types of coloration found in insects have been dealt with in a comprehensive paper by Hagen (1883). Hagen reviews all the published statements regarding

the nature of color in insects and then contributes much from his own researches. Since that time numerous papers have appeared dealing with the subject of insect color, but it would be impossible to review them here. Hagen divided insect colors into: (1) dermal or cuticula colors; and (2) hypodermal colors. Tower (1903) published additional data, especially through morphological studies on the hypodermal and cuticular layers. I have made morphological studies on the body wall of Perillus and find much in common with the figures published by Tower, exhibiting details of the hypodermis and cuticula of Coleoptera.

The present studies on Perillus, as well as an examination of other species of Heteroptera, show that the black and brown colors are located in the cuticula and are not subject to change, once the adult stage has been attained. The white, yellow, and red colors are located in the hypodermis and show through where the black coloring matter is not present in the cuticula. The white color occurs in the absence of pigment granules or globules in the hypodermal cells, while in the yellow and red varieties the hypodermal cells are filled to a greater or less degree with minute colored globules. My breeding experiments with Perillus show that the accumulation of pigment globules in the hypodermis is influenced largely if not entirely by the physiological activities of the bug. And the physiological activities of the bug are governed very largely by the temperatures to which it is subjected. With some insects the kind of food taken would be expected to influence the color, but in the case of *Perillus bioculatus* the food uniformly consists of the body fluids of potato beetles and their larvæ.

The hypodermal colors are subject to change during the active life of the insect. But the change of color in adult bugs is always in one direction, from white to red, or from yellow to red; in other words an accumulation of pigment may take place, but this is never diminished. Once the yellow or red color has been attained in the hypodermis of the adult, it remains throughout the life of the bug. Large numbers of adult bugs have been kept under observation, at both high and low temperatures, but in no case has the red color been decreased. The case is different with growing nymphs. During the last three nymphal instars the yellow color may change to red, or under other conditions, notably high temperatures, the red of a fourth stage nymph may change to yellow, and from that to

white in the fifth instar. Thus the color pattern of an adult is determined largely by conditions under which the nymph has developed; for once having attained the adult stage, the cuticular, or black color pattern cannot be changed, while the hypodermal colors can change only in one direction, white to red, or yellow to red, as the case may be. It is interesting to note that once the red pigment is laid down in the hypodermis of the adult, it is never diminished, thus it must be protected from oxidation.

Of particular interest is the change of color in an adult of the white color form. In this variety a yellow stage can scarcely be detected, for the appearance of color in the white pattern is almost immediately that of red. It is also noticed that the red color appears first at basal angles of pronotum, tip of scutellum, apex of corium (Plate XXIV, Fig. 2), and ventral areas of the abdomen. From these points it progresses outward until in the final stages all the white areas may appear deep red (Plate XXIV, Figs. 4-5). Male specimens turn red much more rapidly than do the females, and in fact it is difficult to keep white males as much as two weeks without the red color developing in the hypodermis. An examination of the hypodermis at points where the red color is just appearing, shows that the globules in the hypodermal cells are yellow at first, but change very soon to red, or at least by the time the cell is well filled with globules. It appears that once these pigment globules have formed in the adult hypodermis, reduction never takes place.

The typical yellow color form (Plate XXIV, Figs. 11-12) has the hypodermal cells filled with minute yellow globules. Under certain conditions, notably temperatures of 78° F., or above, this color may be maintained unchanged. When the temperature goes below 75° F. for a few days, the yellow color begins to take on an orange red cast, and if the bug lives six or seven weeks it may become deep red in color. During hibernation there appears to be no change in color of the bugs, and this is just as might be expected since the physiological processes are at a standstill. It also shows that temperature of itself cannot affect changes in color, but only by influencing physiological processes during the active life of the insect.

RELATION OF TEMPERATURE TO COLOR FORMS.

Experiments were begun in 1916 for the purpose of determining what influence temperature may have on the color pattern of the bugs. These earlier experiments, and many others performed since that time, all indicate the same result, namely, that at high temperatures (85° to 95° F.) the white color form is produced, while at temperatures below 78° F. the yellow and red color forms appear. When the bugs were reared at a temperature of 85° F. or higher, an occasional yellow male would appear but never a red one. At temperatures of from 78° to 82° F. conditions are such that the color pattern of a bug can scarcely be predicted. It is under such conditions that the individual activity of the bug plays a part in determining the color pattern. From what is known of the pigments concerned, and these will be considered shortly, it seems perfectly clear that the rate of metabolism in the individual bug is the factor which determines how much pigment will be laid down in the hypodermis and cuticula. I will also try to show that physical activity of the bug affects this metabolism. A difference in metabolism between the sexes would appear to account for the fact that at temperatures between 78° and 82° F., most of the females will be white and black, while nearly all the males will be yellow and black or red and black. It seems reasonable to suppose that since the female must mature large numbers of eggs the physiological processes, or metabolism, go on at a higher rate than is the case in the male. Also a certain amount of pigment is deposited in the egg. Male specimens of the white color form have never been reared except with temperatures averaging above 82° F. In the male sex then, the only way of raising the physiological activity to a point where white color forms appear, is by rearing the bugs under high temperatures, (85° or higher).

The effect of limiting the physical activity of growing nymphs is indicated by the following experiment. Nymphs were reared in five small tubes of which this is one (¾ in. by 2 in.), and kept at a temperature averaging 88° F. Thirteen adults emerged, of which 6 males and 3 females were of the red and black color pattern; 2 males were classed as yellow and black, while one male and one female were of the white and black color pattern. I had never before reared a red and black

female at a temperature as high as 88° F., and the only explanation for these red forms appearing at such a high temperature appears to be due to the cramped quarters which limited the physical activities of the developing nymphs. Several other bugs reared beside them with the same temperature but in larger cages, all developed the white and black color pattern. It might be added that the humidity was the same for both lots.

On Plate XXIV, Fig. 22, is shown a fifth stage nymph of the typical white color pattern, developed in a temperature of 88° to 90° F. On August 17, this nymph was placed in a cage kept at a temperature of 70° F. By August 20 the nymph had acquired a distinctly reddish color bordering the dark areas of the thorax, as shown (Plate XXIV, Fig. 23). August 22 this same nymph molted to the adult stage and appeared as a yellow and black individual, (Plate XXIV, Fig. 17). The original lot of white nymphs kept at a temperature of 88° to 90° F. all emerged as typical white and black adults. I have in this vial three fifth stage nymphs of the white color form which were placed in a temperature of 70° F. during five days of the last instar, and all of them show a deposit of red pigment in the thorax and ventral areas of the abdomen. These nymphs surely would have emerged to the adult stage with a yellow and black pattern as did others which were allowed to complete their development at a temperature of 70° F.

Since a maximum amount of pigment is deposited in the body wall under low temperatures (65° to 75° F.), and the minimum amount deposited under high temperatures (85° to 95° F.), it appears that increased metabolism does not produce pigment, but on the contrary, must consume or otherwise dispose of the materials which under lower temperatures are laid down as pigment in the body wall.

RELATION OF HUMIDITY TO COLOR FORMS.

While it has appeared rather conclusive that temperature is the chief controlling factor of metabolism and pigment formation in *Perillus bioculatus*, it seemed highly desirable to experiment with relative humidity as a factor separate from temperature. Accordingly, during the past summer an experiment was carried out, that of rearing bugs at a constant high temperature of 90° to 95° F., but in chambers where a high

relative humidity of 87% could be compared with a low relative humidity of 27%.

Time and space will not permit of a detailed description of the apparatus used in the experiment, but briefly it was this: Within the cabinet where the desired temperature was maintained with little more variation than two degrees Fahrenheit, there was arranged a series of glass cylinders connected by rubber tubing, and through them air of a known relative humidity could be drawn. I hold in my hand a single cylinder (2 x 10 in.) or unit of this system, and through this and similar cylinders with which it was connected, a constant stream of air was drawn by means of a water motor. A series of twelve cylinders or breeding cages was set up and connected so that air of approximately 27% relative humidity could be drawn through the first six cylinders, while air of not less than 87% relative humidity could be drawn through the last six cylinders. This was accomplished by first drawing all the air through concentrated H_2SO_4, which removed excess moisture, and then passing the air through a saturated solution of lithium chloride, approximately 27% relative humidity was picked up. After circulating this air through the first six cylinders it was led off and down through two bottles of saturated salt water solution, after which the air was found to carry approximately 87% relative humidity. This air was then conducted through the remaining six glass cylinders where bugs were to be reared. The humidity of the air was checked at different intervals by simply replacing one of the original cylinders by one fitted with wet and dry bulb thermometers; then by speeding up the water motor it was found that an accurate reading of the relative humidity could be made. The top of the cabinet was fitted with two sliding plates of glass and above this a 100-watt lamp kept the rearing chambers constantly lighted.

Six lots of bugs were reared to maturity in these chambers where the relative humidity was controlled. Each lot of bugs represented the progeny hatched from a single egg mass, half of which were placed in a cylinder supplied with air carrying 27% relative humidity, and half in a cylinder of the other series where the relative humidity was kept at 87% or slightly higher. Much difficulty was experienced in rearing all the bugs to maturity due to the extremes of humidity maintained in the experiment. Many casualties occurred at the time of molt-

ing. With a humidity of 27% the bugs found it difficult to molt, and many were dried up in the process. In the cages maintained at 87% relative humidity some of the nymphs in molting were gummed up by the excessive moisture, especially during the early stages. From the six lots reared, 36 bugs reached maturity; 16 were reared in cages having 27% relative humidity, while 20 bugs matured in 87% relative humidity. All the bugs reared were of the white and black color pattern, except five males, which were yellow and black. Three of these yellow males were reared in 27% relative humidity, while the other two were in 87% relative humidity. To this number may be added 44 nymphs of either fourth or fifth instar which died in the molting process, but not before it was possible to determine the color pattern which would have resulted. Of these nymphs, 25 were reared in 27% relative humidity and all were of the white and black color pattern; 19 were reared in 87% relative humidity, of which five were classed as yellow and black forms, while the remainder were of the white and black pattern. The five yellow and black forms all developed in one cylinder which apparently was stuffed with too much gauze to permit of free and normal exercise of the bugs. These bugs had changed from red to yellow, but at a rate much slower than was the case with bugs in other cages. As a check against the bugs reared in the temperature cabinet, many of the eggs not used in the humidity experiment were reared in the laboratory at room temperature of from 70° to 78° F. Under these conditions 61 bugs were reared, classed by color pattern as follows: White and black pattern, 6 females; yellow and black pattern, 3 males and 11 females; red and black pattern, 16 males and 25 females. These bugs came from the same parents that furnished eggs for the experiment with relative humidity.

Such results would seem to indicate that humidity as a factor separate from temperature, does not have much effect on the color pattern of *Perillus bioculatus*. A relative humidity near 100% probably slows up the physical activity of the bugs, and in this way we might expect a greater deposit of pigment. Apparently, humidity can affect the color pattern only by influencing the physical activity of a bug, which in turn affects metabolism.

Up to the present point I had contented myself with the study of the biological problems presented by the color pattern

of *Perillus bioculatus*. I was first concerned with making a study of the color varieties from the genetic standpoint, only to find that in the color pattern of Perillus we are dealing with factors which at best might be termed "environmental characters." The second line of attack was to gain an understanding of the ecological factors which influence or govern the production of color in the body wall of Hemiptera. Having worked out the biological aspects of this problem to my own satisfaction, the single remaining mystery was, what are the pigments concerned?

During the past year I was fortunate in gaining the friendly cooperation of Dr. L. S. Palmer, chemist and authority on Carotinoid pigments, for the chemical examination of the red pigment found in Perillus and a few other Hemiptera. The chemical data obtained are published elsewhere (Palmer and Knight, 1924), but to make this story complete I might briefly review the results. The yellow and red pigment deposited in the hypodermis of *Perillus bioculatus* was found to be carotin, although a trace of water soluble pigment was detected, but the intensity of the color, yellow or red, depends on the concentration of carotin. Since the bug feeds only on the lymph of Leptinotarsa grubs and adults, it was of interest to see if the predaceous bug obtained the pigment direct from its food. For chemical analysis, 5½ c. c. of blood was collected from about 200 larvæ of the potato beetle. This lymph was obtained by pricking the body wall of the grub, taking only one or two drops that oozed freely, and care being taken to stop before the fat bodies emerged. Qualitative and quantitative determinations were made which showed that a single pigment, carotin, was responsible for the golden yellow color of the blood. Strange to say not a trace of xanthophyll could be detected. Dr. Palmer's determinations showed that 0.0136 per cent of carotin was present in the lymph. This is an astonishingly high concentration of carotin for an animal fluid and equals that found in many fresh green leaves.

The potato beetle larva, with its blood literally saturated with carotin, must obtain the pigment from the carotin-rich potato plant. The predaceous Perillus, feeding on potato beetle blood, obtains a supply of pigment which can be eliminated only under the most favorable circumstances. It has been shown by several workers (Palmer, 1922) that the caro-

tinoid pigments oxidize readily in animals having a high rate of metabolism. Furthermore, it might be added that all experimental evidence so far secured points to the fact that carotin is to be regarded as a fortuitous substance in animal forms, to be eliminated as best the animal may. Being a readily oxidizable substance it seems reasonable to assume that oxidation is one of the normal paths of elimination in Perillus. This viewpoint is further supported by the fact that while Perillus feeds on the highly pigmented lymph of *Leptinotarsa decemlineata* Say, the white color forms will, while living under optimum high temperatures and not depositing carotin in the hypodermis, pass a chalky white excreta, thus showing nearly complete oxidation of the pigment, except for small amounts of carotin deposited in eggs by the females. The same white bugs will when placed in a cool environment (70° to 75° F.), pass dark red to brown and black excreta and at the same time begin to deposit carotin in the hypodermis. *In the case of Perillus then, it appears that the physiological activity of the insect which is modified by the temperature is oxidation, influenced by the physical activity of the insect, and that this is the fundamental explanation of the pigment variations.*

Finding carotin to be the sole pigment concerned in producing the visible yellow and red colors in the hypodermis of *Perillus bioculatus*, we extended our examination to include several red and black species belonging to other families of Hemiptera. Chemical examination of the red pigment was made for the following species: Family Miridæ, *Lopidea staphyleæ sanguinea* Knight, and *Coccobaphes sanguinareus* Uhler; Reduviidæ, *Eulyes illustris* Stal, a chiefly red large assassinbug from the Philippine Islands; Lygaeidæ, *Lygaeus kalmii* Stal; Coreidæ, *Leptocoris trivittatus* (Say); Aphididæ, *Tritogenaphis rudbeckiæ* (Fitch), a beautiful vermillion colored species.

The surprising result of these analyses was in finding that the red color in the bugs mentioned, is not due to carotin, but to water soluble pigments, of which two kinds were found (Palmer and Knight, 1924b). The aphid, *Tritogenaphis rudbeckiæ* (Fitch), owes its vermillion color chiefly to an anthocyanin-like pigment, although small quantities of carotin are also present in the bug. In all the other species mentioned, the red color was found to be due to a flavone-like pigment.

From these examinations it would appear that a majority of the yellow and red colored Hemiptera owe their coloration to water soluble pigments, rather than carotin. It also seems probable that the bugs obtain the red pigment directly or indirectly from plant food.

Observations made on *Lopidea staphyleæ* Knight, *Neoborus amoenus* Reuter, and *Horcias dislocatus* (Say), indicate that in these species the behavior of the water soluble red pigments to temperature and metabolism, is very similar to that of carotin in *Perillus bioculatus* Fab. The red color, and likewise the black pigment of the cuticula, is decreased at high temperatures, and increased with lower temperatures. I have some evidence to show that when the temperature is suddenly lowered on a fifth stage nymph of a white color form of *Perillus bioculatus*, the black pigment, or melanin, is formed more rapidly than is the accumulation of carotin (Plate XXIV, Fig. 9).

THE BLACK COLOR PATTERN.

In Perillus, Deraeocoris, Lygus, and a few other Hemiptera observed, the behavior of the black pigment, or melanin, runs parallel with the behavior of carotin in Perillus, that is, decreased at high temperatures and increased with lower temperatures. Efforts were made by some of the earlier workers to establish a connection between the yellow or red pigments of the hypodermis with the melanin of the cuticula, but more recent chemical work shows that the carotinoid pigments, and water soluble pigments, are not the materials from which melanin is derived.

As mentioned above, the black pigment of the color pattern is located in the cuticula, and among the leadidg chemists this pigment is now generally conceded to be melanin (Gortner, 1911). In the present work no attempt has been made to study the chemistry of melanin, but certain observations made on the behavior of this pigment when rearing bugs under high and low temperatures, may be of interest. In the white color form of Perillus (Plate XXIV, Fig. 1), it will be noticed that the black color pattern is reduced to its minimum area, while the white areas are correspondingly larger. In this color form it will also be noticed that the usual black color of the legs has changed to brown while the same is largely true of the black areas of the pronotum. In many specimens of the white color

form the basal area of the pronotal disk shows very nicely a gradation of light brown into dark brown to black; thus exhibiting how normally black areas may appear light brown, due to a very thin deposit of melanin in the cuticula. An examination of numerous specimens indicates very clearly how a slight deposit of melanin in the cuticula appears brown, while in greater concentration the pigment appears black.

Since the white color form is produced at the higher temperatures (85° to 95° F.) when metabolism is carried on at the maximum rate, it becomes clear that the amount of melanin deposited in the cuticula is greatly reduced under these conditions. The decrease of melanin in the color pattern runs parallel with the decrease in deposit of carotin in the hypodermis. While it could not be said that melanin as such is oxidized in a manner similar to carotin, its decrease in the color pattern might be explained through elimination or oxidation of some chromogen in the blood which is necessary for the production of melanin. From the biochemical and physiological viewpoint the production and behavior of the pigment melanin in Perillus would also be the same in other insects that exhibit this pigment in their cuticula.

Such being the case it will be of considerable interest to the taxonomist to know that variations in the black color pattern of Hemiptera, and doubtless other insects, are produced by changes in physiological activity of the insect; and this rate of physiological activity, or metabolism, is governed chiefly by the temperature to which the individual insect is subjected. If we may draw comparisons from the behavior of the color pattern in *Perillus bioculatus* (Fab.), *Neoborus amoenus* Reuter, *Deraeocoris quercalbae* Knight, and *Lopidea staphyleæ* Knight, we may also conclude in the case of many other species which exhibit similar color variations, that the paler forms owe their condition of color to rather high temperatures in their particular environment, while the darker forms are produced during periods of lower temperature, or by some unusual condition which would cause physical inactivity of the insect. This will hold true or else we must believe in the variability of the physiological processes of the protoplasm involved in the production and deposition of melanin in the cuticula of insects.

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EXPLANATION FOR PLATE XXIV.

Adults and nymphs of *Perillus bioculatus* (Fab.), illustrating the various color patterns which occur in this species. All specimens drawn to the same scale (enlarged X 2½) to show relative size of individual bugs.

Fig. 1. Female, typical white color form; legs shown with brownish, although more frequently the legs may be black and still have the hemelytra retain the white color pattern.

Fig. 2. Female, white color form; showing beginning of red pigment (carotin) formation in the hypodermis of the adult bug.

Fig. 3. Female, white color form; showing later stage of red pigment formation than that shown in Figure 2.

Fig. 4. Female, white color form; showing advanced stage of red pigment formation. The usual white areas of the adult white color form have here become deep red due to the deposition of carotin in the hypodermis; this accumulation of carotin taking place during a period of three weeks while the bug was subjected to temperatures of 70° to 78° F.

Fig. 5. Male, white color form, showing advanced stage of red pigment formation in the hypodermis. This male is comparable to the female shown in Figure 4, but the males turn red more rapidly than the opposite sex.

Fig. 6. Female, white color form, but unusual in that the hemelytra show an increase in black pigment over the typical white form as shown in Figure 1. In this bug the formation of melanin was increased over that of the usual white color form but without a visible deposit of carotin in the hypodermis. This with similar examples (Fig. 9) seem to indicate that melanin formation begins at a slightly higher temperature, or accompanying a higher rate of metabolism, than is the case for the formation of carotin in the hypodermis. Then it might be said there is a stage in metabolism of the bug where carotin is still oxidized while melanin formation shows an increase.

Fig. 7. Female. This represents an unusual color form, developing from a fifth stage nymph of the white color form, which for two days before emerging to the adult stage was exposed to temperatures of from 70° to 75° F. Similar treatment of a male bug (Fig. 17) for five days resulted in malanin formation to such an extent that the usual pale areas of the wing were eliminated.

Fig. 8. Female, white color form; illustrating unusual red pigment (carotin) formation in the pronotum. Ordinarily, when adults of the white color form are subjected to lower temperatures (70° to 78° F.) carotin is deposited in the hypodermis at tip of scutellum and apically in the hemelytra just as rapidly as takes place in basal angles of pronotum.

Fig. 9. Female; unusual example of a white and black color pattern. This color pattern apparently develops from a fifth stage nymph which is all set to produce a white color form, but due to a lowering of the temperature for two or three days preceding emergence of the adult, enough melanin is formed to produce black hemelytra, but without carotin deposition taking place. This bug represents a more advanced stage of melanin formation than that shown in Figure 6.

Fig. 10. Female. This bug was upon emergence to the adult stage, similar to the specimen shown in Figure 9. After living several days at temperatures ranging from 70° to 78° F., deposition of carotin occurred in the hypodermis to produce the deep red color as shown.

Fig. 11. Male; typical yellow and black color form.

Fig. 12. Female; typical yellow and black color form.

Fig. 13. Female; orange red color form. This color form may be produced direct from the nymph, or under prolonged conditions of cool temperatures (70° to 78° F.) the yellow and black adult form as shown in Figures 11 and 12, may deepen in color by addition of carotin until the orange red hue is attained.

Fig. 14. Female; typical red and black color form. This form may develop from rearing nymphs at temperatures of from 70° to 75° F., or the yellow and black adults (Figures 11 and 12) may, when kept three or four weeks at the same cool temperatures, gradually change to the deep red color form.

Fig. 15. Male; typical red and black color form.

Fig. 16. Male; red and black color form produced at temperatures near 70° to 75° F., but much reduced in size due to undernourishment.

Fig. 17. Male. This yellow and black male developed from a nymph which went through the color stages shown in Figure 22 and Figure 23. This specimen is very similar to the ordinary yellow and black color form (Figs. 11 and 12) which normally develops from a yellow nymph such as is shown in Figure 24.

Fig. 18. Male. Unusual color form which is suggestive of the color pattern found in *Perillus splendidus* Uhler.

Fig. 19. Male. Rare color form, showing how the normal black spots on anterior half of pronotum have united with the black at base, but still leaving the median line pale or yellow.

Fig. 20. Male. Rare color form, developed with lower temperatures than the normal. Progeny reared from dark forms such as this were normal in color, that is, yellow and black, or white and black, with temperatures ranging from 80° to 90° F.

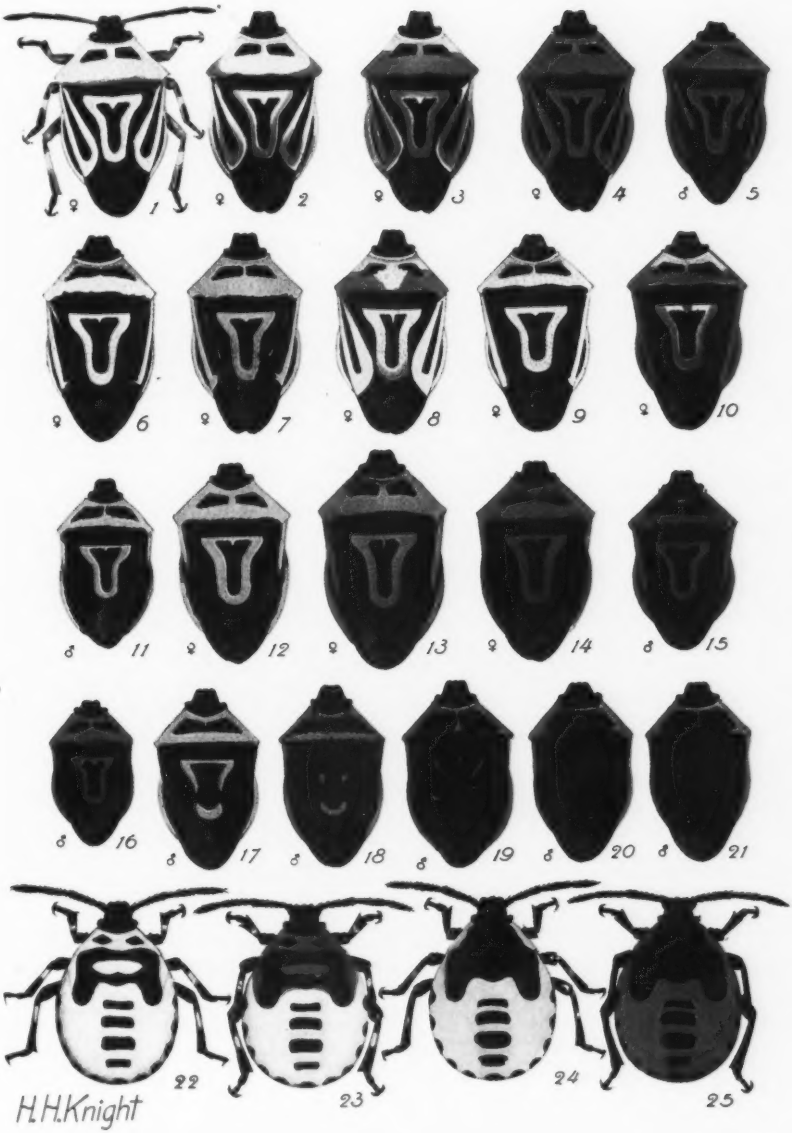
Fig. 21. Male. Rare color form, showing a more extended deposition of melanin in the cuticula than that in Figure 20. This represents the blackest specimen observed.

Fig. 22. Fifth stage nymph of the white color form, reared at a temperature of 88° to 90° F. Such nymphs produce adults similar to that shown in Figure 1.

Fig. 23. Fifth stage nymph of the white color form, which on August 17 was similar to that shown in Figure 22, before it was placed in a cage kept at a temperature of 70° F. By August 20 this nymph has acquired a distinctly reddish color bordering the dark areas of the thorax as shown, also the ventral areas of the abdomen appeared red. On August 22 this same nymph molted to the adult stage and appeared as a yellow and black individual reproduced in Figure 17.

Fig. 24. Fifth stage nymph of the yellow color form. Such nymphs normally produce yellow and black adults, forms shown in Figures 11 and 12.

Fig. 25. Fifth stage nymph of the red color form. Such nymphs normally produce red and black adults as are shown in Figures 14 and 15. With a rise in temperature during the last two or three days of nymphal development, this same nymph would get rid of some carotin and produce an adult similar in color to that shown in Figure 13.



***Perillus bioculatus* Fabr.**

Harry H. Knight

THE COMPARATIVE MORPHOLOGY OF THE MALE GENITALIA OF THE PRIMITIVE LEPIDOPTERA.*

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INTRODUCTION.

The primitive Lepidoptera discussed in this paper include the Jugate Lepidoptera, (Hepialidæ and Prototheoridæ), the Jugo-frenate Lepidoptera, (Mnesarchaeidæ, Micropterygidæ, and Eriocraniidæ), and the Frenate superfamilies Tineoidea, Euceleoidea, and Bombycoidea.† The object in this discussion is to compare the male genitalia of these groups of Lepidoptera with each other and with those of nearly related orders of insects, and to ascertain from this comparison the value of these organs in gaining a more complete knowledge of the natural relationships of the insects treated.

HISTORICAL SURVEY.

References to the male genitalia of Lepidoptera are to be found in the works of such early writers as Malpighi, Swammerdam, and Reamur. Malpighi, (1669), briefly described the male genitalia of Bombyx mori in connection with his discussion of the reproductive system in this insect. Swammerdam, (1737), in much the same manner outlined the gross structure of the genitalia in the European butter-fly, *Vanessa urticæ*. Reamur, (1742), described the physiology of the reproductive system in male Lepidoptera, but made little effort to describe the genitalia. The works of these authors are characterized by a tendency to emphasize the physiology of the reproductive system with little or no description of the external armature which comprises the genitalia.

The first detailed description of the reproductive organs in the microlepidoptera was by Suckow in 1828. This author described these organs in Tinea pellionella, but contributed

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†This division of the Lepidoptera is adopted from Tillyard (1919) and although not quite as logical as that of Packard (1895) seems best adapted for use in this paper.

practically nothing toward the morphology of the genital appendages.

The works of Burmeister, (1832), Kirby and Spence (1838), and Siebold and Stannius (1848) illustrate the first detailed attempts to describe the external and more visible parts of the genital armature. In these the term valvæ or valves was used to denote the two lateral outer appendages. Burmeister (1870, '74) makes further use of this term in describing the genus Euryades and specified that these valves were appendages of the eighth urite, a conclusion arrived at through his failure to count the first abdominal somite.

De Haan (1842), in describing the genitalia of the Paplionidæ used the Dutch term, "kleppen," for the valves and designated the inner lateral appendages as "zijdelingsche aanhangels."

Scudder and Burgess (1870) called attention to the asymmetry of the male genitalia in certain species of Nisoniades and added a few new terms which described certain parts quite specifically. The term "clasp" was used instead of valve; the process arising from the basal portion of the clasp was called the "basal process," and the dorsal portion of the genital armature was named the "upper organ." The terms "main body" and "dorsal crest" were used rather interchangeably for the proximal portion of the upper organ and the distal half was referred to as the "apical portion." The figures accompanying this paper are clear and leave no doubt as to the identity of the parts described. It is also of interest to note that these authors were among the first to emphasize the usefulness of the genitalia as specific characters expressing their confidence in the reliability of them for the purpose of distinguishing closely related species.

In 1876 Buchanan-White published the first comprehensive survey of the male genitalia of Lepidoptera under the title "Of the Male Genital Armature in the European Rhopalocera." In this work the term "harpago" was used for the valve and "tegumen" for the "upper organ" of Scudder and Burgess. This paper and the one by Gosse (1883) had a marked influence in the developing of a comprehensive system of nomenclature for the male genitalia in Lepidoptera and in stimulating future work in this field.

Gosse was influenced by the divided condition of the lateral appendages in the Papilionidæ to use the term valve for the

entire appendage and to restrict the term harpe to "those portions which project freely into the enclosed space between the valves." The term "uncus" was added to describe the hook-like tip of the tegumen and "scaphium" for the "mass of shining white tissue apparently in organic union with the lower surface of the uncus near its origin."

Subsequent to the work of Buchanan-White and Gosse the investigation of the male genitalia of Lepidoptera followed two rather distinct lines of endeavor. In the first of these the authors described the genital appendages in certain genera or groups, using them as characters for the separation of species; in the second, the morphology and ontogeny of these organs were described for the purpose of comparison in more comprehensive, yet related, groups. Of the former, the works of Hoffman (1888, '95), Smith (1889, '98), Pierce (1909, '14, '22), Busck and Heinrich (1921) and Heinrich (1923) are among the most important from the standpoint of the microlepidopterist. Hoffman's descriptions of the genitalia of the Butalidæ illustrated the first serious attempt to describe the external genital armature of such small insects. Smith demonstrated the value of the harpes for separating closely related species of Noctuidæ and inspired Pierce to make a more comprehensive study of the genitalia in this family. Pierce's extensive works on the Noctuidæ, Geometriidæ, and Tortricidæ are the most comprehensive accounts of the genitalia in these groups up to the present time and serve as the basis for work being carried on by present day investigators. Busck and Heinrich have adopted Pierce's system of nomenclature in describing the genitalia in new species of North America Lepidoptera and Heinrich, in his recent revision of the Eucosminæ, has effectively applied the genital characters in clearing up many of the difficult problems in the natural relationships of the members of this group.

In the second class of investigators Cholodkovsky (1885), Peytoureau (1895), Stitz (1900), Zander (1903), and Petersen (1900, '04)* are most worthy of consideration. Cholodkovsky's description of the genitalia in the Adelid moth,

*The works of this author have come to my attention since the writing of this manuscript and are included in the bibliograhhy. In his paper on the significance of the genitalia in the differentiation of species he discusses at length the morphology of the male genitalia and adopts the terminology of Zander (1903), adding the term "fultura penis" to describe the processes associated with the ventral surface of the "ring wall." In the terminology adopted in this paper these are called the "juxta."

Nemotois metallicus Pod., illustrated an early attempt to comprehend the genital system in an insect which because of its minute size and vestiture of scales offered an excellent chance for the development of delicate technique. This work served as the basis for future investigations on the internal genitalia in Lepidoptera and Trichoptera which will be referred to later. Cholodkovsky's treatment of Nematois exhibits a keen and correct insight into the structure of the genitalia. He expresses his regret in being unable to find a system of nomenclature for the genitalia in the literature of his day and proceeds to originate one which admirably serves his purpose. He recognizes the "vinculum" of present day authors as the ninth sternite, and the tegumen as the combined ninth and tenth terga, the latter being rudimentary or "embryonic." For the valves he uses de Haan's term, kleppen, and suggests that they may represent larval appendages which were suppressed in the pupa, i. e., the "schwanzlappen" which Tichomiroff (1880), described in the pupa of Bombyx mori. Cholodkovsky describes the penis as a hollow chitinous rod which enters the ninth somite through a membranous tube, the "praeputium," re-enforced ventrally by a flat chitinous plate, i. e., the annellus and juxta of Pierce. He applies the term "eichelposterchen" to the membranous tip of the penis, i. e., vesica of Pierce, and noted that it was eversible.

The work of Peytoureau comprises a number of extensive treatises on the comparative morphology of the genitalia in the more important insect orders. His study of the Lepidoptera includes six species, and while these were all macrolepidoptera, it is of importance because his conception of the morphological units is based on a study of the pupal development and the nervous system of the genital appendages. He regards the tegumen as being composed of the fused ninth and tenth terga which are distinct and unfused in the pupa. He calls attention to the close connection of the valves, the ninth sternum, and the basement membrane, (anellus), in the pupa, and he regards the penis as the chitinized terminal portion of the ejaculatory duct. He describes the formation of the saccus or median process of the anterior margin of the ninth sternite in Bombyx mori and considers it part of the membrane between the eighth and ninth sterna. With regard to the nervous system, he showed that the genitalia were ennervated by the

"sixth lateral" and the "post terminal" nerves of the last abdominal ganglion, the former supplying the muscles of the base of the ninth sternum and valvæ and the latter the tegumen, the anellus, and the retractor muscle of the penis.

Stitz, using the nomenclature of Buchanan-White, described the genitalia of a series of Lepidoptera in a manner very similar to Cholodkovsky's treatment of Nematois. Of the species included as microlepidoptera, four were Tineoidea.

The work of Zander is probably the most important contribution to the morphology and ontogeny of the male genitalia of the Lepidoptera. He correlated the nomenclature of Buchanan-White and Gosse with the morphological units comprising the genitalia by comparing the adult structures in a large number of moths and butterflies and tracing their development in the larval and pupal stages of a more generalized species. His work on the Lepidoptera was preceded by investigations of a similar nature on the Hymenoptera (1900), and Trichoptera (1901), and through his conception of a common plan of structure for the genitalia in these orders he correctly interpreted the various modifications of identical parts without introducing a large and cumbersome nomenclature. In the Tineoidea seventeen species were examined, of which four were Micropterygidæ, three Adelidæ and Incurvariidæ, and one Tineidæ.

His investigation of the ontogeny consisted of a careful examination of the larval, prepupal, and pupal stages of a Pyralid moth, *Paraponyx stratiatoria*, based on the previous work of Peytoureau, Verson and Bisson (1896), and Klinkhardt (1900). By tracing the development through each larval instar from the very first he improved upon the results of these investigators and recorded the following observations: The male genitalia are formed and develop in a pouch on the ventral side of the hind margin of the ninth somite formed in the first instar by an invaginating of the ectoderm of that region. This pouch was first observed in *Pieris brassicæ* by Herold (1815) and later in *Bombyx mori* by Verson and Bisson. These authors regarded this pouch as a part of the intersegmental membrane between the ninth and tenth somites, but Zander shows that it is actually a portion of the ninth sternum through its relation to the underlying muscles. During the third instar this pouch enlarges into a flask-shaped pocket and a pair of

conical buds develop at the bottom. In the fourth instar these divide, giving rise to a dorsal outer pair and a ventral inner pair. In the last instar the latter unite to form the embryonic penis, and the former migrate to the caudal margin of the ninth sternum. At pupation with the disappearance of the genital pouch these outer buds lie at the surface in close connection with the ninth sternum and form the embryonic valves.

At this stage the penis is invaginated in a second depression which Zander calls the "penis pouch" and through its deepening and the enlargement of the penis the anellus is formed. This Zander calls the "ring wall." During this stage in the pupal development the tenth somite which was suppressed at pupation by the telescoping of the last two abdominal segments of the larva develops a dorsal and ventral appendage, the uncus and the gnathos. These enlarge to form a hood above and below the anus. The lumen of the penis which was formed when the two inner buds united at the bottom of the genital pouch grows deeper as the penis lengthens, eventually ramifies the entire organ and is joined to the caudal end of the ejaculatory duct.

Shortly before the emergence of the adult the parts of the genitalia are chitinized, the deposit of chitin being most heavy on the tegumen, uncus, gnathos and vinculum. The ventral wall of the anellus is chitinized in some species, thus forming the juxta, while in others the entire anellus becomes a chitinous cone. The base of the penis fuses with the portion of the pocket surrounding it and assumes a heavy coat of chitin, leaving only the short connection to the ejaculatory duct and the extreme distal end membranous. After this the parts become covered with hair and scales and the genitalia assume the appearance of the definitive structures.

These results of Zander have made clear the significance of the parts of the genitalia and served as the basis for a uniform system of nomenclature suggested by McDunnough in 1911. This author recommended the adoption of a set of terms to be determined by the law of priority for scientific names, a law which does not apply to morphological nomenclature. Consequently his terminology has not been adopted by all workers on Lepidoptera. It differs little from that of Pierce and in the following description of the parts comprising the genitalia I have included his terms whenever they were equivalent to those of Pierce.

Aside from descriptions of the morphology of the genitalia of the Lepidoptera in the literature of this order many references of value will be found in general literature on insect morphology and particularly in the contributions relating to the genital system. A discussion of such literature would be quite voluminous and aside from the purpose of this paper. However, the contributions of Walker (1922), and Crampton (1918, '19, '20, '21, '22) are of particular interest because these authors have compared the male genitalia throughout all the lower insect orders up to and including the lower Lepidoptera. The nomenclature used by them is a compilation of the terms used by Berlese (1882, 1906, '09), Escherisch (1903, '04), Heymons (1895, '96, '99, 1912), Verhoeff (1903), Verson (1904), and others, and is compared with that adopted for the Lepidoptera in a subsequent table. Both of these authors have reached the conclusion of Zander regarding a fundamental plan of genitalia structure common to all insects. They have homologized the genital appendages very thoroughly throughout the orthopteroid and neuropteroid insects and their allies and from this have deducted certain conclusions regarding their phylogeny. Such of these orders as show particular relationships to the Lepidoptera are discussed in a subsequent section of this paper.

Nomenclature.

Reference has already been made to the contributions of Pierce, Busck, and Heinrich to the nomenclature of the male genitalia of the Lepidoptera. Although Busck and Heinrich have not adopted all of the terms which Pierce uses in his more recent descriptions of the Geometriidæ and Tortricidæ, or those suggested by McDunnough, the system which they have applied to North American Lepidoptera differs so little from those of Pierce and McDunnough that, in view of the fact that they have contributed more than have any other authors to our knowledge of these organs in the native species, it has seemed best to adopt their terms in this paper. In defining these terms in a subsequent section of our discussion we have pointed out the equivalent terms of Pierce and McDunnough.

The works of Walker and Crampton, previously mentioned, form the basis for the most recent comparison of the genitalia of orthopteroid and neuropteroid insects. The system of nomen-

clature used by them may be readily homologized with that of Busck and Heinrich and is used in the section of our discussion dealing with a comparison of the genitalia of the Orthoptera, Neuroptera and Lepidoptera. To make these terms readily

COMPARATIVE TABLE OF SYSTEMS OF NOMENCLATURE USED BY BUSCK AND HEINRICH, WALKER AND CRAMPTON, AND ZANDER.

BUSCK AND HEINRICH	WALKER AND CRAMPTON	ZANDER
Tegumen	Ninth Tergite or Epiproct	Ninth Tergite (Ruckenschuppe)
Uncus	Epiandrium or Epiproct (In part)	Dorsal appendage of the tenth somite; Uncus
Gnathos	Paraprocts?	Ventral appendage of the tenth somite; scaphium
Socii	Surgonopods (Neuroptera, Mecoptera and Trichoptera)	Lateral prolongations of the postsegmental margin of the ninth tergite; Anal appendages
Vinculum	Ninth sternite; Hypandrium (when forming a plate); Coxasternum (in part)	Ninth sternite
Saccus	.....	Medio-ventral projection of the ninth sternite; Saccus
Harpes	Gonapophyses, or Gonostyli* (in Orthoptera)	Appendages of the ninth sternite; Valvae
Transtilla	.....	.....
Anellus	Parameres (in part) Epiphallus?	Portion of penis pouch surrounding the penis where it enters the genitalia; Ring wall
Juxta	Pseudosternite?	Chitinized venter of the Ring Wall
Aedoeagus	Phallus, Penis or Aedeagus	Chitinized outer end of the penis
Penis	Ejaculatory Duct	Ductus Ejaculatorius

comparable and to show their relation to the morphological units of the genitalia as determined by Zander, the systems of Busck and Heinrich, Walker and Crampton, and Zander are tabulated below. The nomenclature originally applied by

*Crampton regards the Harpes as the terminal portion, or Gonostyli, the coxites having fused with ninth sternum.

Walker and Crampton to the Orthoptera has been subjected to many changes by the latter author as his conception of the significance of these structures in the different insect orders became clearer. This has led to the correction of certain terms originally misused and the replacement of others by new ones which the author thought more applicable. There has resulted a cumbersome and poorly organized system from which I have selected only the most reliable terms for use in the comparative table and in the discussion of the orthopteroid and neuropteroid genitalia.

A Description of the Parts Comprising the Male Genitalia in Lepidoptera.

The following structures ordinarily comprise the male genitalia in Lepidoptera and can be recognized and homologized throughout the different families. (See Fig. 1.)

Somites: The abdomen of the Lepidoptera consists of ten distinct segments or somites, each of which, with the exception of the tenth, possesses a distinct tergum and sternum. Ordinarily somites 1–8 undergo little modification. Occasionally the chitin of the terga and sterna of certain somites is interrupted by circular, membranous orifices, which are referred to as "fossæ" in subsequent discussion. Sometimes the seventh and eighth sterna bear prominent hair pencils or tufts (Haartaschen, Poljanec, 1901), which are concealed in membranous pockets of the intersegmental membrane. Similar structures have been described on more anterior segments in the Sphingidæ et al. In some Rhopalocera lateral processes arise from the posterior margin of the eighth sternite (Rami, Stickel, 1899), and the Bombycidæ usually possess an armature of hooks and processes on this segment. In the Scythrididæ, Gelechiidæ et all, the eighth sternum and tergum are separated along their lateral margins and form a ventral and dorsal hood over the genitalia. In the Plutellidæ the eighth sternum is divided on the median line and the lateral lobes thus formed surround the genitalia.

Genitalia: The genitalia proper include the highly modified ninth and tenth somites and are composed of the following parts:

Tegumen, (Buchanan-White, 1878)*: This term is applied to the tergal portion of the ninth somite which forms the dorsal part of the genitalia. It articulates laterally with the ninth sternum, the suture frequently being solidly fused. The anus opens directly below the caudal margin of the tegumen and is largely concealed by it.

Tenth Somite: This somite is usually membranous and retracted but in the Micropterygidæ and Adelidæ Zander and Cholodkovsky have described the tergum as a small terminal sclerite separated from the ninth by a distinct suture. In such generalized forms the absence of the uncus allows a normal development of the dorsal portion of this usually suppressed somite. The anus opens at the terminal end of the somite and in most Lepidoptera where the segment is entirely membranous it is indistinguishable from the distal end of the anal tube.

Uncus, (Gosse, 1883): This and the following two parts constitute the anal armature and belong to the tenth somite; because of its retraction however, they assume a superficial attachment to the tegumen. Zander has shown that when these processes are developed the tenth somite remains membranous throughout the entire development of the genitalia serving only as the base for their attachment. In shape the uncus is hook like, spoon shaped, clavate, emarginate, bifed or trifed; it is usually heavily chitinized. In the primitive Lepidoptera it is often absent or reduced to a small hook which over arches the anus.

Socii, (Pierce, 1914): These are paired organs, normally soft, membranous, and hairy, which arise from the tegumen on each side of the anus. They are absent in most of the primitive Lepidoptera but occur almost invariably in the more specialized families.

Gnathos, (Pierce, 1914) = (Scaphium, Gosse, 1882): = (Subscaphium, Pierce 1909). This also is a paired organ which arises from the tegumen near the base of the uncus. When complete it consists of two lateral arms which surround the anus and a median ventral plate situated directly below the anus. It is subject to great modification, the ventral plate often being reduced or absent. In many of the families treated in this discussion it is entirely missing.

Vinculum, (Pierce, 1909) = (Saccus, in part, Baker, 1891): This term is applied to the ninth sternite which usually takes the form of a ventral chitinous band articulating with the tegumen at its lateral margins. In the Micropterygidæ and Eriocraniidæ it differs little in width from the tegumen and is often solidly fused with it; in the Aculeate Tineoidea it is much longer than the tegumen, U or V-shaped and more heavily chitinized. The opposite tendency prevails in the higher groups where the vinculum is often reduced to a narrow transverse band which connects the bases of the harpes.

The anterior margin or apex of the vinculum is often produced anteriorly to form a medio-ventral chitinous sack which lies beneath the

*Buchanan-White's use of the term tegumen included both the tergum and sternum; later the sternum was called the saccus by Baker, and the vinculum by Pierce, so the term tegumen is now restricted to the tergum and is equivalent to the upper organ of Scudder and Burgess.

eighth sternite. The name "Saccus" was applied to this structure by Baker in 1891 and Pierce, 1914, in revising his terminology, applied it to the vinculum and saccus combined. Since Baker's original use of the term "Saccus" applied to the invagination rather than to the entire ninth sternum we prefer to adopt McDunnough's suggestion and apply the term vinculum to the entire ninth sternum whether or not its margin is produced to form a saccus. The saccus occurs in most of the Tineidæ and nearly allied microlepidoptera as well as in many Bombycoidea and Rhopalocera.

Harpes, (Smith, 1890) = (Valvæ, Burmeister, 1832): These are paired clasping organs which articulate to the posterior margin of the vinculum. Often too their bases are closely associated with the juxta and in many Hepialidæ are articulated to it. In most primitive Lepidoptera the harpes are symmetrical, although there are frequent exceptions. They are normally triangular, finger like, or spoon shaped. In many families, especially among the higher Lepidoptera, the harpes are divided into three distinct lobes or areas, a dorsal, apical and ventral, called by Pierce the costa, valvula or cucullus, and sacculus. In the Noctuidæ, et. al. the sacculus and costa frequently develop appendages or processes which become so widely separated from the remainder of the harpess that they have been described as separate structures. The "clasper" of Smith and the "ampulla" of Pierce come under this class but because such modifications occur so rarely in primitive forms need not be extensively discussed in this paper. Occasionally the harpes are greatly reduced and fused with the vinculum so closely that they are practically functionless as claspers, e. g. Eriocraniidæ.

Reference has already been made to the investigations of Zander on the development of the harpes in which he showed that they are appendages of the ninth sternum which arise from the lateral buds of the genital pouch and during pupal development, migrate to the periphery, and become attached to the ninth sternum.

Transtilla, (Pierce, 1914): In most Lepidoptera this structure occurs in the form of a chitinized band or bridge which connects the inner costal angles of the harpes passing just below the gnathos and behind the ædœagus. Sometimes it is lobed and ornamented with spines.

The above parts have been called by Pierce the "external part" of the genitalia and constitute the accessory armature. The following structures are called the "internal part" and comprise the intromittant organ and its armature.

Anellus and *Juxta*, (Pierce, 1914): The anellus is the cone-like tube through which the penis enters the ninth somite. It is usually membranous, often covered with spines and bears a triangular or quadrate plate, the juxta, on its ventral surface. The lateral margins of the juxta may be produced to form hairy lobes or the central portion elongated into a process which supports the ædœagus. Occasionally the entire anellus is chitinized forming a funnel or perforated plate through which the ædœagus protrudes.

Aedœagus, (Pierce, 1909): This structure ordinarily consists of a chitinous tube which enters the ninth somite through the anellus and is

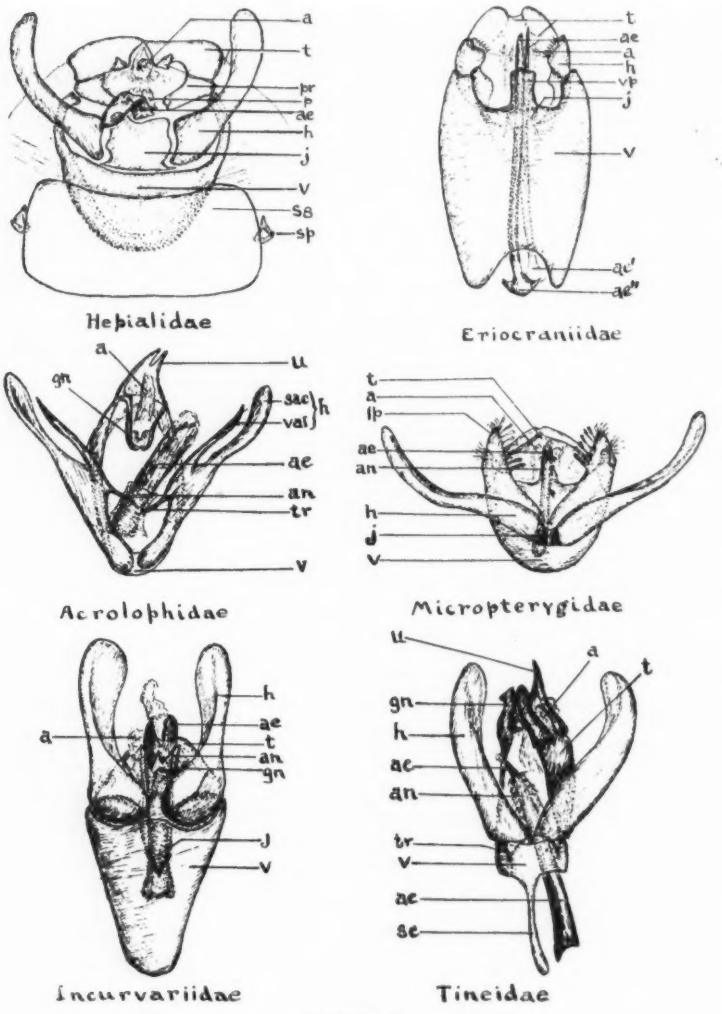

FIGURE I.

Ventral Views of the Male Genitalia of Primitive Lepidoptera illustrating homologies and the arrangement of parts. (semi-digrammatic).

Abbreviations: a—anus; ae—ædœagus; ae'—dorsal wall of ædœagus; æ''—ventral wall of ædœagus; an—anellus; gn—gnathos; h—harpe; j—juxta; lp—lateral process of tegumen; p—penis; pr—caudal process of tergumen; s8—eighth sternum; sac—sacculus; sc—saccus; sp—spiracle; t—tegumen; tr—transtilla; u—uncus; v—vinculum; val—valvula or cucullus; vp—median process of vinculum.

supported by it and the juxta. It is heavily chitinized, frequently armed with spines and serrations and has the posterior end inflated to form a blind pouch in which are lodged the retractor muscles of the penis. Zander has shown that the ædœagus is the chitinized terminal portion of the penis and its bulbous base is formed from the modification of the penis pouch. In the Hepialidæ the ædœagus occurs as a flat plate and the membranous penis passes behind it and opens at its caudal margin.

Penis, (Busck and Heinrich, 1921) = (Ductus ejaculatorius, (Pierce, 1914): This term applies to the terminal portion of the ejaculatory duct which lies within the ædœagus. It is a soft eversible tube which may be projected by blood pressure beyond the tip of the ædœagus and serves to introduce the sperms into the bursa copulatrix of the female. This eversible tip is called the "vesica," Pierce, 1914, and is often armed with spines or clusters of spines called "cornuti."

The arrangement of the above described structures in the most common types of genitalia which occur in the primitive Lepidoptera are illustrated in Fig. 1.

A Comparison of the Lepidopterous Type of Male Genitalia With Those Found in Insects of Nearly Related Orders.

In this discussion we wish to show that the type of male genitalia which prevails in the Lepidoptera is to be found in a somewhat modified condition in those insects most nearly related to them, i. e., the Trichoptera, Neuroptera and Mecoptera. The plan of structure in this type has its origin in the most primitive insect forms and has been traced by Walker and Crampton in its various modifications through the Thysanura, Ephemerida, and Orthoptera. As certain of these forms are in the direct line of development toward the type found in Lepidoptera, they will be discussed in detail under the various insect orders in which they occur.

Thysanura and Ephemerida.

The genitalia of these two orders may be conveniently discussed together because they possess many points in common and furnish a generalized, basic, type of genitalia from which may be derived the types found in the other insect orders. In the Thysanura as illustrated by Machilis, (Text Fig. II, 1) the ninth sternum is quite small and completely hidden by the coxites of the eighth. It bears two large coxites each with a terminal stylus. These are homologous with the coxites and styli of the Ephemerida, (Text Fig. II, 3), and with the harpes of the

Lepidoptera and the gonopophyses of related orders. In the Ephemerida the coxites possess two or three segmented styli which become clasper-like just as do the gonopophyses of the higher insects, and develop prominent basal muscles for their manipulation.

In certain species of the genus Heptagenia, i. e., *flavescens* Wlsh., and *tripunctata* Banks, the ninth sternum is slightly produced between the coxites and suggests a ventral plate or "hypandrium" which is characteristic of many Orthoptera, Neuroptera and Mecoptera.

In both orders the ninth tergum is an unmodified transverse sclerite rounded laterally and articulating with the pleura.

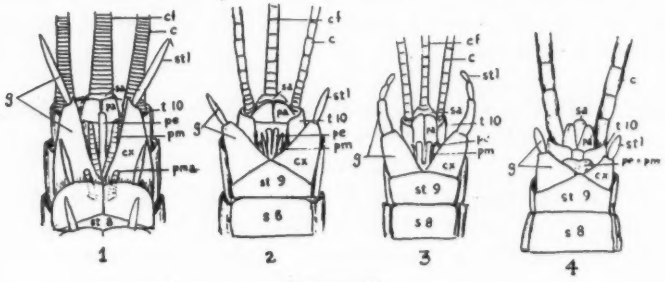

FIGURE II.

Ventral Views of Male Genitalia of Thysanura, Ephemerida and Orthoptera (after Walker).

1—Machilis; 2—Hypothetical primitive type; 3—Ephemerid; 4—Grylloblata nymph.

Abbreviations: c—cercus; cf—caudal filament or telofilum; cx—coxite of ninth sternite; cx8—coxite of eighth sternite; g—gonopophysis which is composed of cx, the coxite and stl, the stylus; pa—paraproct; pe—penis; pm—posterior paramere or its main process; pma—anterior paramere; sa—supra-anal plate; stl—stylus; s8—8th sternite; s9—9th sternite; t9—9th tergite; t10—10th tergite.

In the Thysanura the tenth somite is well developed and bears three caudal appendages, the two lateral ones, the cerci, and a central one, the telofilum or cerciform appendage. The anus opens beneath these. Crampton, (1921), in homologizing these structures with the terminal appendages of Isopod Crustacea, considers the basal segment of the telofilum as homologous with the eleventh somite, the remaining segments as the telson, and the cerci and their basal plates, the paraprocts, as the vestiges of a pair of biramous limbs in which the protopodite is represented by the paraproct, the endopodite by

the cercus, and the exopodite is lost. Wheeler's work on the embryonic development of Xiphidium, (1893), also supports the view that the cerci and their basal plates represent the eleventh somite, and its appendages. The same arrangement of the tenth and eleventh somites obtains in the Ephemerida. In this order, however, there is a medium shelf-like structure suspended beneath the anus. Walker has homologized this with the subanal vomer of the Phasmidæ and it resembles very closely the gnathos of Lepidoptera and similar subanal structures of the Neuroptera and Trichoptera.

The penis of the Thysanura is a single, median, membranous or lightly chitinized, tube re-enforced laterally by a pair of chitinous processes, the parameres. In the Ephemerida these parts are fused forming a median, membranous structure which possesses two efferent ducts. Walker considers this type as the more primitive of the two and believes that the generalized insect ancestor possessed two penes, each with a separate ejaculatory duct, just as the females of certain Thysanura still retain double genital apertures.

From this brief survey of the genitalia of these two orders it will be seen that they are constructed along the same general plan and that the Ephemerida, although retaining a more primitive type of penis, tends to develop a large ninth somite provided with forcep-like coxites and styli, thus forshadowing the clasping type of genitalia which characterizes the Lepidoptera and its near relatives.

Species examined: *Machilis sp.*, *Heptagenia flavescens* Wlsh., *H. tripunctata* Banks., *H. interpunctata* Say., *Callibaetis ferruginea* Wlsh., *Hexagenia bilineata* Say., *Blasturus cupidus* Say.

Orthoptera.

Close resemblances to the type of genitalia just described for the Ephemerida are found only in the very generalized Orthoptera. Walker (1914 and '19), has described such a form in *Grylloblatta campodeiformis* Walk., (Text Fig. I, 4), from Australia and has given the development of the male genitalia particular attention. It resembles the clasping type of genitalia as described for the Ephemerida in the following respects. The ninth sternum bears on its posterior margin a pair of coxites each with a terminal stylus. Although unsymmetrical in the adult, these are almost alike in the nymph and are movably articulated to the sternum. They possess prominent basal

muscles which Walker believes enables them to function as claspers, thus resembling gonopophyses. The tenth somite and the penis are much the same as in the Ephemerida and need not be discussed except to state that the latter is composed of two papillæ with a single, central, ejaculatory duct. In the remainder of the Orthoptera the coxites are suppressed or fused with the ninth sternum, the penis is complicated and unsymmetrical and the entire genitalia depart greatly from the simple type of Grylloblatta.

Plecoptera and Odonata.

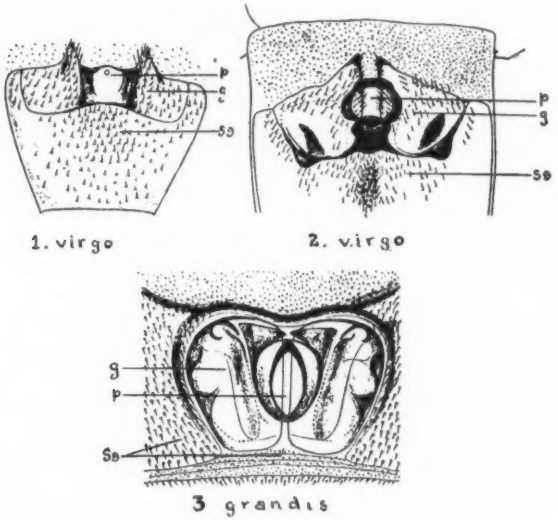

FIGURE III.

Ventral views of the male genitalia of Odonata (after Van der Weele).

1—Calopteryx virgo L., nymph; 2—C. virgo L., adult; 3—Aeschna grandis L., adult.

Abbreviations: g—gonopophysis; p—opening of the ejaculatory duct or homologue of penis in other insects; s9—9th sternite.

The adults of these orders bear little resemblance to the generalized genitalia just described because the ninth and tenth somites retain the ring-like structure of the preceding somites and coxites and styli are not developed. The nymphs of the Odonata (Text Fig. III, 1) however, bear small appendages on the caudal margin of the ninth somite which Van der Weele,

(1906), has homologized with the gonopophyses of the higher insects. In the adult (Text Fig. III, 2 and 3) these are greatly reduced and form small plates on each side of the opening of the ejaculatory duct, and the large appendages developed on the tenth somite which are usually called gonopophyses in the taxonomic literature are not in any sense homologous with the true gonopods of other insects.

Neuroptera.

The male genitalia of this group show such a wide diversity of structure that it is difficult to select a series of forms which will illustrate the transition from the generalized genitalia of the Ephemerida and Grylloblattoidea to the more specialized types which are characteristic of the Mecoptera, Trichoptera and Lepidoptera. By selecting the more generalized representatives of each of the natural subdivisions of the order and discussing in detail each structure comprising the genitalia, rather than the complex, some idea can be obtained of the extremely synthetic nature of the genitalia in this order and of the generalized type from which so large a number of diverse forms has been derived.

Crampton has discussed in detail the morphology of the genitalia of the Neuroptera and homologized the parts with those of the Mecoptera, Trichoptera, and Lepidoptera. His conclusions regarding the homologies are in the main correct, but unfortunately he has not examined the more primitive members of many of the groups and has failed to gain a conception of the true significance of many of the structures which he figures. He has also apparently ignored the excellent figures which Van der Weele, (1910), and Ebsen-Peterson, (1913, '21), give in their revisions of the Megaloptera and Mecoptera which furnish the various steps in the lines of genitalia specialization occurring in these groups.

For convenience the general characters of the genitalia of the Neuroptera are outlined below while their special morphology is discussed under the various families into which the order is divided.

General Characters: Ninth sternum enlarged and produced to form a ventral plate or so called hypandrium beneath the genitalia, thus crowding the gonopophyses dorsad so that they are often closely associated with the anus. The penis is either

a membranous papilla through which the ejaculatory duct opens, a pair of papillæ with the opening between them, or a chitinous plate or process with the duct opening at its base. The simple papilla type resembles that in the Ephemerida and Grylloblatoidea, while the plate and process types are closely analogous to that of the Jugate Lepidoptera, except that in the latter the duct opens at the posterior margin of the plate. In none of the Neuroptera do we find a hollow, tube-like penis such as is characteristic of the Trichoptera and most Lepidoptera. In the following discussion of the special morphology the family divisions of Van der Weele are used for the Megaloptera, and those of Ebsen-Peterson (1906), and Comstock (1918) for the Neuroptera Planipennia.

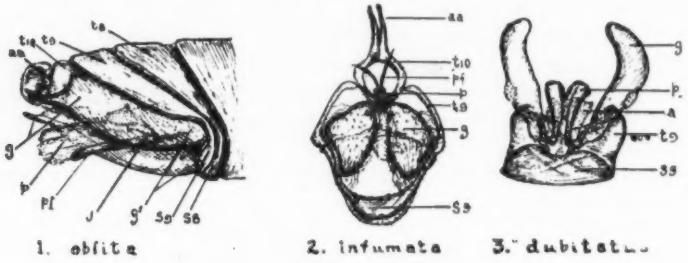

FIGURE IV.

Male genitalia of the Neuroptera, Megaloptera.

1—Raphidia oblita Hag., right side; 2—Sialis infumata Newm., venter; 3—Archichauliodes dubitatus Walk., venter.

Abbreviations: a—anus; aa—anal appendages; g'—base of gonopophysis; g—gonopophysis; j—armature of base of penis; p—penis; pf—filamentous process of penis; pl—ventral plate of penis; s8—8th sternite; s9—9th sternite;t9— 9th tergite; t10—10th tergite.

Megaloptera: There is no clear-cut series of genitalia characters which will distinguish this group from the Planipennia. The more generalized tendencies seem confined to the Sialidæ and Raphididæ of the Megaloptera, while the specialized ones occurring in the other families simply are carried further in the Planipennia.

Raphididæ: (Text Fig. IV, 1). The genitalia of this family are the most generalized of the Neuroptera and foreshadow many of the characters occurring in the Trichoptera and Lepidoptera. The ninth sternum is not produced to form a hypandrium, but is emarginate and bears a pair of large

gonopophyses on its posterior margin; these are ventral in position, thus differing from the gonopods of most Neuroptera which tend to become lateral or dorsal. The gonopophyses are entire, (*R. oblita* Hag.), emarginate, or deeply cleft, (*R. xanthostigma* Rostock). The penis is either an elongate, membranous papilla chitinized on the venter, (*R. oblita*), or an irregular papilla with several fleshy protuberances, (*R. xanthostigma*). The ventral chitinization in *R. oblita* is basally connected with the gonopophyses and suggests the juxta of Lepidoptera. This type of penis is the closest approach in the Neuroptera to the chitinized tube of the Trichoptera and Lepidoptera. The tergum of the ninth somite is transverse and unmodified; the tenth and eleventh somites are represented by a dorsal plate which over arches the anus and bears a pair of short unsegmented processes, possibly the rudimentary cerci. Species examined: *R. xanthostigma* Rostock, *R. oblita* Hag.

Sialidæ: (Text Fig. IV, 2). The genitalia of this family are less generalized than those of the preceding, but several features suggest close homology with the Raphididæ and with the Lepidoptera. The ninth sternum is slightly produced and forms a short hypandrium, thus forcing the gonopophyses dorsad so that they are lateral in position and articulate with the pleural region of the somite. They are triangular or quadrate in shape and suggest the harpes of the Aculeate Tineoidea, i. e., Adela or Nepticula. The penis consists of a pair of fused chitinous plates often bearing terminal spines, or a pair of papillæ. The tenth and eleventh terga are indistinguishably fused and terminate in a pair of processes. In the European species of Sialis these are short, recurved, and heavily chitinized and resemble a bifid uncus.

Species examined: *Sialis infumata* Newm., *S. lutaria* L.

Corydalidæ: The remaining Megaloptera are grouped in this family under two tribes, the Neurotomini and the Chauliodini, the first characterized by a longitudinal dividing of the gonopophyses into a dorsal and ventral portion, which gives them the appearance of two separate pairs of gonopophyses and the second by the reduction and dorsal migration of the gonopophyses so that they appear as small plates closely associated with the anus. Most of the species of this family have been figured by Van der Weele and Crampton and need not be described. Archichauliodes, (Text Fig. IV, 3), is the

most generalized member of the family having undivided gonopophyses which are large and clasper-like, a small ninth sternum, and a penis consisting of two chitinized processes with a single ejaculatory opening between them.

Species examined: *Archichauliodes dubitatus* Wlk., *Parachauliodes japonicus* Mc. L., *Chauliodes pectinicornis* L., *Nigronia serricornis* Say., *Hermes maculipennis* Gray. *Chloronia hieroglyphica* Ramb., *Corydalus cornutus* L.

Neuroptera Planipennia: The male genitalia of this group closely resemble the types found in the Neurotomini and the Chauliodini. The Mantispidæ, Ascalaphidæ and Myrmeleonidæ are further specializations of the type found in Corydalis of the Neurotomini, the Hemerobiidæ may be derived from Archichauliodes, and the Polystœchotidæ, Osmylidæ, and Sisyridæ are modifications of the Hemerobiid type. The Nemopteridæ

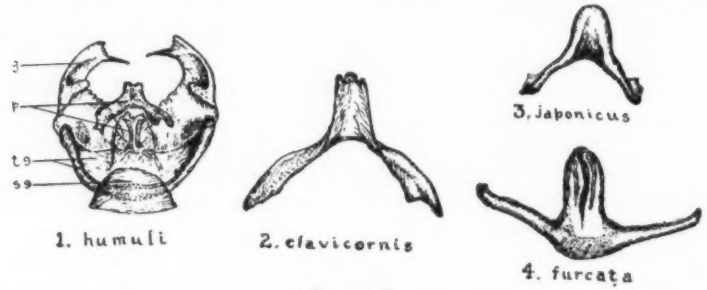

FIGURE V.

Male genitalia and penis of Neuroptera Planipennia and Megaloptera.

1—Hemerobius humuli L., venter; 2—Tomateres clavicornis Hag., penis; 3—Parachauliodes japonicus McL., penis; 4—Albardia furcata Van der Weele, penis.

Abbreviations: g—gonopophysis; p—penis; s9—9th sternite; t9—9th tergite.

are modified Hemerobiids with Drepanepteryx as an intermediate form, and the Coniopterygidæ are also close Hemerobiid relatives from the viewpoint of genitalia structure. Of these families the Hemerobiidæ (Text Fig. V, 1), represent the most generalized type. The penis of all the Planipennia and some Megaloptera (Parachauliodes) superficially resembles that of the Hepialid Lepidoptera and a series of these are figured for comparison. (Text Fig. V, 2, 3, and 4).

Species examined:

Mantispidæ: *Mantispa interrupta* Say., *M. formosana; Climaciella brunnea* Say.

Ascalaphidæ: *Albardia furcata* Weele., *Colobopterus versicolor* Burm., *Acheron trux* Wlk., *Hybris javana* Burm., *H. subjacens* Wlk., *Deleproctophylla australis* F.

Myrmeleonidæ: *Tomateres clavicornis; Achanthaclisis distincta; Palpares caffer* Burm., *Myrmeleon* sp.
Hemerobiidæ: *Micromus timidus* Hag., *M. angulatus* Stph., *M. posticus* Wlk., *Boriomyia concinnus; B. subnebulosus* Stph., *Hemerobius humuli* L., *H. micans* Ol., *H. strugosus* Zh., *H. stigmaticus* Fh., *Drepanopteryx phalænoides* L.
Polystœchotidæ: *Polystœchotes punctatus* F.
Nemopteridæ: Nemoptera lusitanica Lch.
Osmylidæ: *Osmylus maculatus* F., *O. multipunctatus* Ml., *O. tuberculatus; Climacia areolaris* Hag.
Sisyridæ: *Sisyra vicaria* Wlk., *S. fuscata* F.
Chrysopidæ: *Leucochrysa varia* Schd., *Ankylopteryx 8-punctata* F., *A. borneensis* Weele.
Coniopterygidæ: *Coniopteryx psociformis.*

Mecoptera.

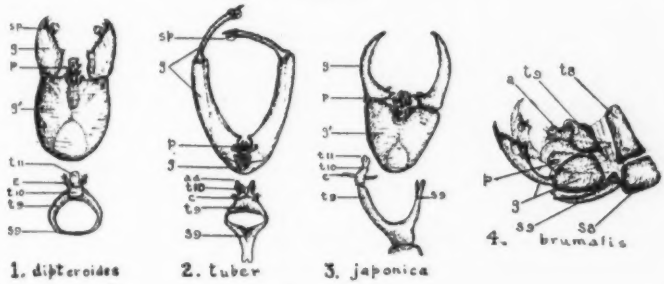

FIGURE VI.

Male genitalia of the Mecoptera (views ventral unless otherwise specified).

1—Nannachorista dipteroides Till., 2—Merope tuber Newm., 3—Panorpa japonica Thunb., 4—Boreus brumalis Ftch. right side.

Abbreviations: a—anus; aa—anal appendages; c—cercus; g—gonopophysis; g″—fused bases of gonopophyses; p—penis; sp—sense organ; s8—8th sternite; s9—9th sternite; t8—8th tergite; t9—9th tergite; t10—10th tergite; t11—11th tergite.

With the exception of one family, the Bittacidæ, the male genitalia of the members of this order present many interesting structural characters in common with the Trichoptera and primitive Lepidoptera and form a connecting series between them and the Ephemerida and lower Neuroptera. The general characteristics of the genitalia of the order are as follows: Abdomen with ten well developed somites, the tenth bearing a pair of cerci; ninth sternum usually produced caudad to form a hypandrium; gonophyses two jointed, the basal joints resembling the coxites of the Ephemerida and Grylloblattoidea and the unsegmented distal joint, the styli. The ninth sternum and the coxites are often fused to form a vinculum-like structure which surrounds the penis which is a chitinized or membranous tube often armed with spines or processes. The special morphology will be discussed under the various families which Ebsen-Peterson, (1921), uses in his revision of the order, with the addition of the Nannachoristidæ which, following Tillyard's (1919) suggestion is elevated to family rank.

Meropidæ: (Text Fig. VI, 2). The genitalia of this family are the most generalized of the order. The ninth sternum is slightly produced forming a small hypandrium; the tergum is large and transverse and bears a pair of small processes called the dorsivalvæ. The tenth tergum is folded under these and bears the one jointed cerci. The gonopophyses are very long and the terminal joint is toothed at the apex and bears a small sense organ in the notch. These joints articulate with the basal joints so that their movement is toward the meson and at right angles to them. The basal joints are fused proximally on the ventral line forming a small U-shaped structure beneath the penis. The penis is short, heavily chitinized, and consists of a pair of basal processes which are fused with the gonopophyses and four distal processes or spines which project caudally between the gonopods.

Species examined: *Merope tuber*, Newm.

Boreidæ: (Text Fig. VI, 4). The genitalia of this family differ from those of the preceding in the following respects: the hypandrium is larger; the dorsi-valvæ are absent; the tenth somite is represented by the anus and the cerci by small tubercles associated with it; the gonopophyses are shorter with the basal joint heavier and the distal joints fold dorsad so that they lie above the basal ones. Their apices are serrate and the sense organ is rudimentary. Their fused bases are narrow and U-shaped. The penis is membranous and hangs free between the gonopophyses.

Species examined: *Boreus brumalis* Fitch.

Nannachoristidæ: The genitalia of this family are a modification of the type described in Merope and resemble in many respects the genitalia of the Jugofrenate and Aculeate Lepidoptera. The ninth sternum is narrow, transverse, and is not produced into a hypandrium. The tenth and eleventh terga are small rectangular sclerites, the latter of which bears a pair of two jointed cerci. The gonopophyses are very large and the basal joints are entirely fused and form a U-shaped structure very similar to but obviously not homologous with the vinculum in the Aculeate Tineoidea. The distal joints are short, triangular, with a serrate inner margin which bears a sense organ composed of a cup-shaped base and a membranous bulb-like apex. In shape, these closely resemble the harpes of the Aculeate Tineoidea. The penis consists of a short, heavily chitinized ædœagus, terminated with spines and a membranous eversible tip, and is fused with the basal joints of the gonopophyses.

Species examined: *Nannachorista dipteroides* Till.

Panorpidæ: The genitalia of this family (Text Fig. VI, 3) so closely resemble those of the Nannachoristidæ that it is unnecessary to describe them in detail. The figure of Panorpa japonica Thunb. will serve to bring out the morphological features of the group.

Species examined: *Panorpa japonica* Thunb., *Panorpa sp.* (N. A.); *Panorpodes carolinensis.*

Bittacidæ: The genitalia of this family resemble those of the Nematocerous Diptera more closely than any of the Lepidoptera and need not be discussed in this paper.

Trichoptera.

Although the male genitalia of the various families comprising this order are quite diverse, the more generalized families show close structural affinity with those of the Mecoptera and Lepidoptera. In their resemblance to the Lepidoptera it is often difficult to distinguish between superficial similarities and those which are of actual phylogenetic value. Consequently only the more generalized members have been selected for detailed comparison with the primitive Lepidoptera while brief reference is made to the specialized tendencies of the higher families.

The comparative morphology within the order has been exhaustively treated by Zander, (1910), and Klapalek, (1904), and the anatomy of the internal genital system of the male by Stitz, (1904), and Cholodkovsky (1913). The contribution of Zander and Cholodkovsky are of especial interest because they have included in their comparisons references to similarities between the Trichoptera and Lepidoptera.

Zander divided the Trichoptera into two well-separated groups which can be distinguished by the structure of their genitalia. The first of these included the family Limnophilidæ and was characterized by a funnel shaped chitinized penis pouch, a membranous retractile penis, terminating in long processes or filaments, small gonopophyses or valvæ, and very large anal appendages. The second group which included the remaining families possess an opposite set of characters, i. e., a membranous penis sheath, a penis of which at least the base is chitinous, large valvæ, and small or moderately large anal appendages. The genitalia of the Lepidoptera resemble this second group in the following respects: penis pouch membranous, penis chitinized, with the exception of the Hepialidæ and Prototheoridæ, gonopophyses (harpes or valves) large, and anal appendages, (socii), small. Both orders offer some few exceptions to this set of characters but they hold for the majority of the families. In addition to the above there is a tendency in both orders for the development of a dorsal and a ventral appendage of the tenth somite which as already mentioned are named the uncus and gnathos in the Lepidoptera.

Aside from describing the adult structures Zander worked out their prepupal and pupal development and in his later paper (1903), has compared the manner of development of the various parts in the two orders. His general summary of this phase of his work is as follows: The prepupal development of the genitalia in the Trichoptera is parallel to that of the Lepidoptera with respect to the formation of a genital pouch, the primary differentiation of the penis and harpes, and the migration of the latter to the caudal margin of the ninth sternum. The pupal development of the two is quite different especially with respect to the penis. This structure is developed in a penis pouch, as in the Lepidoptera, but the pouch does not become deeply invaginated and the base of the penis remains linear, and receives the ejacultaory duct at the termen instead of some distance from it.

Cholodkovsky described the structure of the testes, vasa deferentia and accessory glands in the more important families of the Trichoptera

and found, as he had already described for the Lepidoptera, (1884), four distinct types of testes which he named the embryonic, the larval, the pupal, and the definitive, according to their degree of specialization. The first two types he found present in the more generalized Trichoptera and the primative Lepidoptera, i. e., Hepialidæ and Tineoidea, while the two latter more specialized types occurred only in the higher families of both orders. The direct comparisons which he made between certain families will be included in the subsequent discussion.

The general morphology of the external genitalia of the order has been already mentioned in the discussion of the work of Zander. The following additional features noted in our own study should be added before proceeding to the special morphology of the different families. The tergum and sternum of the ninth somite are usually fused to form a solid ring, or the sternum is separated from the fused terga and pleura, and the two structures thus formed are comparable to the tegumen and vinculum of the Lepidoptera. The gonophyses are one or two jointed but the basal joints are never fused together as in the Mecoptera. Occasionally the terminal joint consists of two pieces which articulate side by side to the termen of the basal joint. The penis in all the families except the Limnophilidæ consists of a chitinized tube containing the terminal portion of the ejaculatory duct and is quite similar to the ædœagus of the Lepidoptera. It is armed with spines, filaments or serrations in much the same manner. A chitinized plate resembling the juxta of Lepidoptera often supports the penis on the ventral surface, and in some instances the bases of the gonopophyses are attached to it.

In the subsequent discussion of the special morphology the conception and arrangement of the families according to Ulmer, (1907), has been adopted, along with certain suggestions offered by Dr. Cornelius Betten, (in litteris).

Rhyacophilidæ and *Philopotamidæ:* (Text Fig. VII, 1, 2, 3, and 4). The male genitalia of these two families are quite similar and represent one of the most generalized types in the order. The ninth sternum is either narrow and transverse as in Rhyacophila (VII, 1), or rectangular or U-shaped forming a distinct vinculum as in Philopotamus (VII, 2 and 3), and Chimharra (VII, 4), and in these has a close resemblance to the vinculum of the Micropterygid Lepidoptera. The ninth tergum forms a broad dorsal arch and is fused on the median line with the tenth tergum. In Philopotamus the lateral margins are produced and form lobes similar to the lateral lobes of the tegumen in the Micropterygidæ, although they lack spines and setæ with which the latter are armed. The tenth somite is rudimentary and closely associated with the anus. In Rhyacophila and Philopotamus it bears a median simple or bifed process and two lateral appendages, the anal appendages of Zander, which, as already stated, may be homologized with the uncus and socii of the Lepidoptera. In Chimharra the entire anus is chitinized and only the anal appendages are present. In some species the tenth somite has a ventral appendage resembling the gnathos. The gonopophyses consist of one or two joints articulated to the medio-ventral portion of the ninth sternum. In most species they are joined together at the basal

angles by membrane or a small chitinized bridge, in this respect resembling the harpes of the Micropterygidæ. In no case, however, are the entire basal segments fused to form a V-shaped structure as in the Mecoptera but rather a vinculum, when present, is formed by the enlargement of the ninth sternum as in the Lepidoptera. The terminal portion of the gonopophysis is often emarginate, completely divided, or armed with spines and processes. All of these tendencies are characteristic of the harpes of the Lepidoptera. The penis is usually large and with the basal portion chitinized. The termen is either entirely membranous and eversible, with or without spines, or it is divided into a dorsal and ventral plate and two lateral processes which surround a membranous central portion, i. e., the end of the ejaculatory duct. The ejaculatory

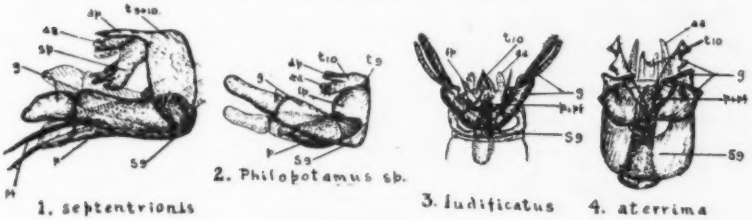

FIGURE VII.

Male genitalia of the Trichoptera: Rhyacophilidæ and Philopotomidæ.

1—Rhyacophila septentrionis McL., right side; 2—Philopotamus sp., right side; 3—P. ludificatus McL., venter; 4—Chimharra aterrima Hag., venter.

Abbreviations: aa—anal appendages; dp—dorsal process of 10th tergite or fused 9th and 10th terga; g—gonopophysis; lp—lateral lobe and process of 9th tergite; p—penis; pf—filamentous process of the penis; s9—9th sternite; sp—subanal plate or process, i. e., homologue of the gnathos of Lepidoptera; t9—9th tergite; t10—10th tergite.

duct enters the apex of the base of the penis except in a few species of Philopotamus where the base is bulb-like and the duct enters on the dorsum.

Species examined: *Rhyacophila septentrionis* McL., *R. sp.* (two N. A. species from the collection of Dr. Betten); *Glossosoma sp.*, *Philopotamus ludificatus* McL., *Chimharra aterrima* Hag.

Hydroptilidæ: (Text Fig. VIII, 1 and 2). The genitalia of this family resemble those of the two preceding but are smaller, with the parts more closely fused, and frequently without gonopophyses. The ninth somite is highly chitinized, the sternum forms a quadrate vinculum, and the ninth and tenth terga are fused to form a hood-like tegumen. The anal appendages and the median dorsal process (uncus), are usually present but quite small. In Agraylea multipunctata Curt. the caudal margin of the tenth tergum forms two large lobes one on each side of the median process and closely resembles the caudal margin of the tegumen in the Eriocraniidæ. The gonopophyses when present are one jointed, but in many species they are absent or indistinguishably fused with

the ninth sternum. A similar reduction and fusion of the gonopophyses occurs in the Eriocraniidæ. The penis is heavily chitinized, usually with an enlarged basal portion and the apex is armed with one or more spines. A type of penis very similar to this occurs in many of the Micropterygidæ, Eriocraniidæ and Aculeate Tineoidea. From the preceding comparison it will be seen that the Hydroptilidæ and Eriocraniidæ present an interesting case of structural parallelism which is in reality of phylogenetic significance. Both families have arisen through the most primitive groups of their respective orders, have become highly specialized through reduction, and have produced as the end product very similar types of genitalia.

Species examined: *Agraylea multipunctata* Curt., *Hydroptila consimilis* Mort., *H. hamata* Mort.

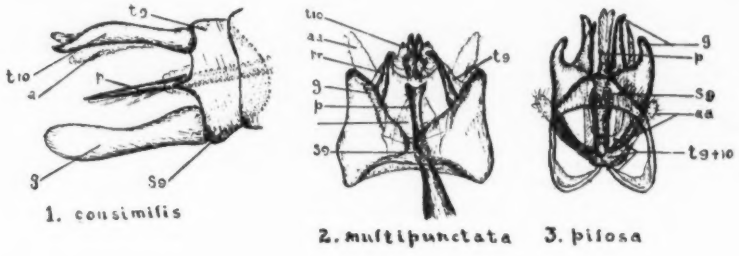

FIGURE VIII.

Male genitalia of the Trichoptera: Hydroptilidæ and Sericostomatidæ.

1—Hydroptila consimilis Mort. right side; 2—Agraylea multipunctata Curt. venter; 3—Goera pilosa Fab. venter.

Abbreviations: a—anus; aa—anal appendages; g—gonopophysis; j—basal armature of penis, i. e., homologue of the juxta of Lepidoptera; p—penis; pr—process of fused lateral margin of 9th somite and gonopophysis; s9—9th sternite; t9—9th tergite; t10—10th tergite.

The genitalia of the Hydropsychidæ, Polycentropidæ, and Psychomyidæ are quite similar and appear to be modifications of the type described for the Rhyacophilidæ and Philopotamidæ. The Calamadoceratidæ and Odontoceridæ also come under this class but are even more greatly modified with respect to the penis and the tenth tergite. None of these modifications have any significance in relation to the Lepidoptera and need not be included in this discussion.

Species examined: *Macronema hyalinatum* Pictet., *Polycentropus sp., Psychomyia sp., Hydropsyche sp., Ganonema sp., Odontocerus sp.* (N. A. species from the collection of Dr. Betten).

Molannidæ and *Leptoceridæ*: (Text Fig. IX, 1, 2 and 3). The genitalia of these families are quite different from those of the preceding families and present a type of structure which presents many features in common with the Hepialidæ, Prototheoridæ, and Mnesarchæidæ of the Lepidoptera. The ninth sternum usually forms a broad, U-shaped

vinculum; the juxta, when present, is contigous to its caudal margin and often fused with it, and the one jointed gonophyses articulate to its lateral margins or on the meso-ventral portion of the vinculum when the juxta is absent, thus duplicating the manner of articulation of the harpes in the Hepialidæ and Mnesarchæidæ. In Beræa, (Text Fig. IX, 3) one of the Molannidæ, the ventral margins of the vinculum bears a median process which resembles a similar structure in the Eriocraniidæ. The ninth and tenth terga are fused and form the tegumen. In Leptocerus (Text Fig. IX, 1), this is produced caudally and forms several lobes which resemble similar tegumen structures in the Eriocraniidæ. The two lateral ones are probably the anal appendages. In the Molannidæ, the anal appendages are more laterally placed, thus resembling the tegumen of the Mnesarchæidæ, while the median portion forms a bifid uncus, a structure which does not occur in the Lepidoptera just

FIGURE IX.

Male genitalia of the Trichoptera: Leptoceridæ, Molannidæ, and Phryganeidæ (all views ventral).

1—Leptocerus dilutus Hag., 2—Molanna angustata Curt., 3—Berea pullata Curt., 4—Phryganea japonica McLach.

Abbreviations: j—basal armature of the penis, i. e., homologue of the juxta and annellus of Lepidoptera; p′—base of penis; vp—median process of 9th sternite; other abbreviations as in Fig. VII.

mentioned. The penis too is quite different from the plate-like ædœagus of the Jugate Lepidoptera. It is a chitinized tube more like the penis of the Micropterygidæ and Tineoidea with an eversible membranous termen which often bears spines.

Species examined: *Leptocerus dilutus* Hag., *L. exquisita* Wlk., *Molanna angustata* Curt., *M. cinerea* Hag., *M. sp.*, *Beræa pullata* Curt.

Phryganeidæ: (Text Fig. IX, 4). This family is usually placed further along in the series, near the Limnophilidæ, but as the genitalia seem to be nearest in structure to those of the Molannidæ and Leptoceridæ it is inserted here. The eighth sternum is usually heavily chitinized, and forms a plate beneath the ninth sternum and the base of the genitalia much as it does in the Hepialidæ and Bombycidæ. The ninth sternum is small, quadrate, and often fused with the inner surface of the eighth. The gonopophyses are small, finger-like, sometimes with a short terminal joint, and are articulated to a small plate, possibly the homologue of the juxta. The ninth tergum forms the dorsal integument and the tenth tergum is a small rectangular sclerite usually closely fused

with it, and produced laterally into spines or processes. The anal appendages are lobate, spine like, or absent. The penis is short, heavily chitinized, toothed or spined, and has an eversible membranous tip also armed with spines.

Zander studied many species of the Molannidæ, Leptoceridæ and Phryganeidæ and made diagrams representing ideal cross sections of the typical genera. In the Leptoceridæ and Phryganeidæ these show the distal ends of the penis pouch and the anus contiguous or separated by thin membrane. This same condition occurs in the Hepialidæ where as already mentioned the membranous penis passes behind the plate like ædœagus and opens directly beneath the anus and the two are separated only by their membranous walls.

The testes of the Molannidæ and the Phryganeidæ were examined by Cholodkovsky (1913), and found to be similar in type to those of Hepialus and Phassus.

Species examined: *Phryganea japonica* McLach., *Neuronia postica* Wlk.

Sericostomatidæ: (Text Fig. VIII, 3). Only two genera of this family were studied, but Zander and Klapalek have described the modifications occurring in the different subfamilies very completely. From a study of their descriptions and the species mentioned below the genitalia of the family show many resemblances to those of the Tineidæ and Acrolophidæ. The ninth sternum forms a quadrate or emarginate vinculum which in one of the subfamilies, Brachycentrinæ, posseses a saccus much like the Telæporine Tineidæ. The gonopophyses are quite broad and are articulated to the lateral angles of the ninth sternum; in Helicopsyche the outer margin is divided and forms a sacculus and cucullus as in the lower Tineidæ, or Acrolophidæ. In Gœra they are emarginate at the apex. The tegumen is composed of the fused ninth and tenth terga and may bear a central process, uncus, or several lateral processes. The anal appendages are usually small. The penis is thin, heavily chitinized, with a bulbous basal portion and a small eversible tip. The ejaculatory duct usually enters the dorsal side of the base. This type of penis is quite like the ædœagus of the Tineidæ or Acrolophidæ.

The testes of Gœra were examined by Cholodkovsky and found to be similar to those of Tinea and Tineola.

Species examined: *Gœra pilosa* Fabr., *Gœra sp.*, *Helicopsyche sp.*

Limnophilidæ: The nature of the specialization in this family has already been mentioned in our review of Zander's work. The peculiar penis and penis pouch, the large anal appendages, and the greatly reduced gonopophyses find no homologues in the Lepidoptera. The genitalia of the sub-family Apataniinæ have gonopophyses and a dorsum very similar to the Rhyacophilidæ showing that the type is a specialization from a very generalized form, probably from the ancestral stock of the order.

Species examined: *Platyphylax sp.*, *Apatania* sp., (Ulmer's figure).

Diptera, Hemiptera and Hymenoptera.

Crampton, (1919, 1920, 1922, (a) and (b)), has described the genitalia in a number of the families of these orders and compared them with those of the Orthoptera, Neuroptera, Mecoptera, and Trichoptera. Since they do not show as close resemblance to the Lepidoptera as do the Mecoptera and Trichoptera and these similarities when they do exist show their relation to these orders rather than to the Lepidoptera; further discussion of them is unnecessary.

The Special Morphology of the Male Genitalia of the Primitive Lepidoptera.

Suborder: *Jugata.*

Hepialidæ: (Plates XXV and XXVI). The male genitalia of this family were treated by the author, (1921), and an effort was made to homologize the nomenclature of Newell, (1918), with that of Pierce. Further study of the family has revealed the incorrectness of Newell's interpretation of the structures in the family and the following list of general characters is substituted.

The abdomen, as in most Lepidoptera, is composed of nine chitinized somites, and a membranous tenth, which is usually without appendages. Somites 3–8 usually bear a number of unchitinized areas or fossæ which also occur on certain somites in the Jugo-frenate Lepidoptera. The eighth somite possesses well developed spiracles; in the higher Lepidoptera these are rudimentary or absent. The eighth sternite is often heavily chitinized and forms a plate beneath the base of the genitalia, and the caudal margins of the eighth and ninth sterna are sometimes fused or articulated together. The eighth tergum in some species is produced caudally and forms a dorsal hood around the genitalia.

The ninth sternum forms the vinculum and is quadrate, U-shaped, or V-shaped. It is sometimes provided with a short, broad saccus. The juxta, a quadrate, chitinized plate, is situated directly caudad of the vinculum and on the mesal line of the venter. The harpes are short, finger-like appendages which articulate with the lateral margins of the juxta or occasionally, in part, with the lateral angles of the vinculum. Ordinarily the harpes are simple but in some species are emarginate, divided, or bear small appendages or processes.

The ninth tergum is large, hood-like, and weakly chitinized, or emarginate on the meson of the caudal margin. The caudal margin bears one or two pairs of processes which may fuse with the ædœagus to form a suspensorium around the penis, or project caudad around the anus. The ædœagus consists of a small, chitinized plate situated on the venter of the terminal portion of the ejaculatory duct or penis and caudad of the anellus. Its caudal margin may be produced into a spine or spatulate process, or the entire plate may be fused with the caudal processes of the ninth tergum. The tenth somite is entirely membranous

and forms the base of the anus, from which it can not be distinguished. In a few species the tergal portion is chitinized and may be recognized from the remainder of the anal tube.

The articulation of the harpes and juxta, the peculiar type of ædœagus, the suppression of the tenth somite, and the caudal processes of the ninth tergite separates this family and the Prototheoridæ from the remainder of the Lepidoptera. On the basis of the species studied the genitalia of the family may be divided into ten groups or subtypes. The first five of these illustrate a progressive series; three of the latter five are derived from one of the former subtypes, while the last two subtypes seem bizarre and isolated.

Subtype I: This group comprises the most generalized forms of genitalia in the family, and is characterized as follows: ninth tergum without large processes; ædœagus small, plate like and with a short, spatulate, median process. In some species the caudal margin of the eighth tergum is produced and forms two small lobes. The vinculum is without a saccus and the eighth sternum is only slightly chitinized. *Hepialus lupulinus* L. (Plate XXV, Fig. 1), illustrates the simplest form of this subtype, and *H. fusconebulosus* Geer., one of the more specialized.

Subtype II: (Plate XXV, Fig. 3). This group is distinguished from the preceding by having the processes of the ninth tergum enlarged and fused with the ædœagus forming a "suspensorium" beneath the penis, and by the presence of a small saccus on the vinculum of many species. Most of the European species of Hepialus may be placed in this group, and *Phassus Schamyli* Chr.

Subtype III: The species of the North American genus Sthenopis form this group, which differs from the preceding one only in the incomplete fusion of the ædœagus and processes of the ninth tergum, and in the more constant occurrence of the saccus.

Subtype IV: (Plate XXV, Fig. 4). The genitalia of this group represent modifications of subtypes I and III, and show considerable variation. The suspensorium is usually incomplete, the processes of the ninth tergum are hook-like or cygnate, and the saccus is small or absent. The harpes are subject to great modification being spined, emarginate or completely divided into a cucullus and sacculus (Plate XXV, Figs. 5 and 2, and Plate XXVI, Fig. 2). Most of the species of the group are from Australia and are classed in three related genera.

Subtype V: (Plate XXVI, Fig. 8). This group, consisting of the species of the Australian genus Oncopera, is characterized by having the contiguous processes of the ninth tergum closely approximated forming an uncus-like structure, by the small quadrate ædœagus, and by the fusion of the vinculum and the eighth sternum.

Subtype VI: (Plate XXVI, Fig. 1). This type is a modification of the former in which the uncus is larger and more clearly defined. The penis lacks the chitinized ventral plate, or ædœagus, and the vinculum is provided with a median, bifed, tooth on the caudal margin. The harpes are battledore shaped and their narrow bases articulate with the large juxta. The African genus Gorgopis forms this group.

Subtype VII: (Plate XXV, Fig. 9, and Fig. 6). The genitalia of this group are characterized by the extreme fusion and chitinization of parts. The processes of the ninth tergum are fused dorsally behind the anus and ventrally beneath the penis, forming the boundaries of a large aperture containing the anus and penis. The juxta and harpes are greatly reduced in size and are forced forward owing to the expansion of the processes of the ninth tergum. The vinculum is often fused with the juxta and with the eighth sternum. The New Zealand species of Porina, and Pielus and Dalaca form this group.

Subtype VIII: and IX: Both of these types seem to be modifications of VII, but are quite different in appearance. In VIII the processes of the ninth tergum form a large funnel-like orifice through which the anus protrudes; the ædœagus is long, slender, and recurved, the harpes are absent, and the caudal margin of the eighth sternum is deeply emarginate. In IX (Plate XXV, Fig. 7).the harpes are present but greatly reduced, the ædœagus is vestigial, and the caudal margin of the eighth tergum forms a large asymmetrical hood consisting of several highly chitinized lobes.

Subtype X: (Plate XXVI, Fig. 6). In this type the genitalia are quite broad, the vinculum is short and quadrate, the anellus is broader than long, the harpes are trunacte, and the ædœagus narrow and recurved, fusing with the pair of narrow processes from the lateral margins of the ninth tergum.

The species which were examined are tabulated under their respective subtypes:

I—*Hepialus lupulinus* L., *H. fusconebulosus* Geer., *Hectomanes simulans* Wlk., *H. crocea* Luc.
II—*Hepialus amasinus* H. S., *H. carna* Esp., *H. gallicus* Ld., *H. sylvinus* L., *H. humuli* L., *Phassus Schamyli* Chr.
III—*Sthenopis argenteomaculatus* Harr., *S. quadriguttatus* Gr., *S. thule* Spr.
IV—*Oxycanus* (Porina) *fuscomaculatus* Wlk., *Hepialus eximius* Scott., *H. variabilis* Br., *H. hectoides* Boisd., *Perrisectis australasiæ* Don.
V—*Oncopera intricata* Wlk., *O. mitocera* Turn., *O. epargyra* Turn. n. sp.
VI—*Gorgopis libania* Stoll., *G. sp.* (Africa).
VII—*Pielus hyalinatus* H. S., *Trictena labyrinthicus* Don., *Porina umbraculata* Guer., *P. cervinata* Wlk., *P. novæ-zealandiæ* Wlk. (*signata* Wlk.); *Dalaca terea* Schaus.
VIII—*Hepialus hecta* L.
IX—*Phassus metellus* Druce.
X—*Hepialus medusa* (Africa); *Palpifer sexnotatus* Moore.

Prototheoridæ: (Plate XXVI, Fig. 4). The genitalia of this family resemble those of the Hepialidæ very closely. The tergum of the ninth somite is provided with a number of recurved processes very similar to those in group IV of the Hepialidæ, the harpes are long and narrow and are articulated to the juxta, which is continuous with the caudal margin of the vinculum. The vinculum is narrow, U-shaped, and without a saccus. The aedoeagus consists of a recurved plate terminated by an elaborate armature which serves to separate the species examined.

Species examined: *Prototheora petrosema* Meyr. and *P. corvifera* Meyr.

Suborder: *Jugo-Frenata.*

Mnesarchaeidæ: (Plate XXVIII, Figs. 3 and 6). The genitalia of this group are intermediate in their structure between the Hepialidæ on one hand and the Micropterygidæ, Eriocraniidæ, and the Aculeate Tineoidea on the other. The absence of a tube-like aedoeagus and the form of the vinculum are suggestive of these structures in the Hepialidæ; the shape and articulation of the harpes is similar to that of the generalized Micropterygidæ and Aculeate Tineoidea, and the dorsal integument resembles the type which occurs in the Eriocraniidæ. The general characteristics of the genitalia are as follows: Tegumen made up of the fused ninth and tenth terga, the tenth remaining entirely membranous; lateral margins of the tegumen expanded forming an inner pair of setose lobes and an outer pair of chitinized finger-like processes. Vinculum broadly U-shaped or quadrate. Harpes triangular, joined to the meson of the vinculum by their inner angles, and to the latus by their outer angles. Juxta, a membranous plate, heavily spined. Aedoeagus, membranous and in *M. hamadelpha* Meyr., terminated by two chitinized spines.

Species examined: *Mnesarchæa loxoscia* Meyr., *M. hamadelpha* Meyr.

Micropterygidæ: The genitalia of this family present a series of types which form a nucleus from which may be derived practically all the forms of genital structure occurring in the Eriocraniidæ and the Aculeate Tineoidea. In the genus Sabatinca alone five distinct types of genitalia occur, all of which foreshadow tendencies which later appear in the Tineoidea. The general characters of the family are as follows: Tegumen large and hood-like, composed of the ninth and tenth terga; uncus, when present, solidly fused with the tegumen; anus membranous; vinculum U-shaped, much longer than broad and in some cases composed of the fused eighth and ninth sterna; harpes spoon-shaped, triangular, or finger-like, often cleft at the apex or with terminal spines, and articulating with the juxta in the meso-ventral portion of the vinculum. Aedoeagus, large, and usually as long as somites 7–9 inclusive, its base chitinized, sometimes enlarged and receiving the ejaculatory duct on the dorsum, as in the higher Lepidoptera, or slightly narrowed and receiving the duct at the apex as in the Trichoptera, termen membranous, eversible, sometimes spined. Anellus, membranous, juxta, composed of a small chitinized plate or bridge which connects the bases of the harpes. Abdominal fossæ consisting of a pair of unchitinized apertures with a heavy chitinous margin and situated on each side of the meson of the fifth sternum. The species of the family may be divided into six groups* based on the types of genitalia.

*Since the writing of this Dr. Alfred Philpott, Cawthron Institute, New Zealand, informs me that he has divided the New Zealand species of the Genus Sabatinca into the same number of groups and has submitted the results of his investigation to the Transactions of the Entomological Society of London under the title, "On the male genitalia in Sabatinca and Allied Genera, with observations on the same structures in Mecoptera." In this he includes a number of species which were not available to me for study and probably anticipates some of the conclusions already drawn from my study of the Nannachoristidæ.

Subtype I: (Plate XXVII, Figs. 3 and 4). Tegumen large, uncus absent, vinculum composed of the fused eighth and ninth sterna; harpes large, spoon-shaped, and articulating with the quadrate, plate-like-juxta on the meson of the vinculum; aedoeagus with the base slightly attenuate and receiving the duct at its apex. The group shows its relation to the Hepialidæ through the retention of a large juxta, and to the Aculeate Tineoidea, Prodoxidæ, and Incurvariidæ, in the shape of the vinculum, tegumen, and harpes.

Subtype II: (Plate XXVII, Fig. 7). This and the next two groups are-modifications of the first. The tegumen bears a long uncus, the harpes are spoon-shaped and cleft at the apex, and the aedoeagus is enlarged basally and receives the ejaculatory duct on the dorsal side; its distal end is armed with short recurved spines.

Subtype III: (Plate XXV, Fig. 8, Plate XXVI, Figs 3, 5 and 7, and Plate XXVII, Figs. 5). Harpes, long and finger-like; lateral margins of the tegumen lobate and armed with spines and setæ; juxta, small and triangular; uncus present in most species and sometimes partially or entirely fused with the lateral lobes of the tegumen, i. e., (Plate XXV, Fig. 8, and Plate XXVI, Fig. 5).

Subtype IV: (Plate XXVII, Fig. 1). This group is composed of the single Australian species of the genus Sabatinca and resembles subtype I, with the following exceptions: The vinculum is shorter and consists only of the ninth sternite and the harpes are slender, finger-like, and deeply toothed at the apex.

Subtype V: (Plate XXVII, Fig. 8). This group is a modification of Subtype I and forms the transition between it and Subtype VI. Tegumen as in I; harpes small, triangular, with the inner angles of their broad bases articulating with a small linear juxta on the meson of the vinculum, and their outer angles to the latus of the vinculum.

Subtype VI: (Plate XXVII, Fig. 2). This group is a modification of the former in which the harpes are more slender and bear a pair of inner processes; the juxta is entirely membranous; the tegumen is emarginate and possesses a small gnathos; the aedoeagus has a subterminal process. Subtypes V and VI represent intermediate forms which connect the generalized Micropterygidæ, as illustrated in Subtype I, with the Eriocraniidæ and the Aculeate Tineoidea, Incurvariidæ, Adelidæ and Nepticulidæ. The species of Micropterygidæ which were examined are tabulated below under their respective Subtypes.

I—*Sabatinca chrysargyra* Meyr., *S. incongruella* Wlk.
II—*Sabatinca aurella* Huds., *S. ianthina* Philp., *S. doroxena* Meyr.
III—*Micropteryx thunbergella* F., *M. aruncella* Sc., *M. sepella* F., *M. calthella* L., *M. ammanella* Hb., *M. rablensis* Zell., *M. Rothenbachii* Frey.
IV—*Sabatinca calliplaca* Meyr.
V—*Sabatinca eodora* Meyr.
VI—*Epimartyria auricrinella* Wlsm.

Eriocraniidæ: (Plate XXVII and XXVIII). The characters of this family are as follows: Fifth sternum with a pair of fossæ as in the Micropterygidæ. Ninth somite a heavily chitinized cylinder, sternum slightly longer than the tergum and forming the vinculum. Anterior

margin of the vinculum deeply emarginate, caudal margin heavily chitinized and often with a median process. Tegumen emarginate at the apex, forming two large lobes which assume the position of a dorsal hood. Zander has labeled these lobes the tenth tergite and their close association with the anus and the presence of a transverse suture between them and the remainder of the tegumen supports this view. Harpes small, triangular or quadrate, with median basal processes which are attached to muscles in the region of the juxta, while their outer basal angles are attached or firmly fused with the lateral margins of the vinculum. Often the harpes are greatly reduced and so fused with the vinculum as to be scarcely distinguishable, i. e., Plate XXVIII, Fig. 2. Juxta large, quadrate, partially or entirely chitinized. Aedoeagus with heavily chitinized dorsal and ventral surfaces and membranous lateral ones so that it assumes the appearance of two separate, narrow, elongate pieces with acute apices; vesica enlarged and plicate; base of aedoeagus enlarged and receiving the ejaculatory duct on the dorsum. Anellus membranous, sometimes with short spines.

The structural resemblances of the genitalia to those of the Micropterygidæ have already been mentioned. The harpes, tegumen, especially the terminal lobes, and the aedoeagus offer reliable characters for the separation of all the species that were examined.

Species examined: *Mnemonica fastuosella* Zell., *M. auricyanea* Wlsh., *M. unimaculella* Zett., *Eriocrania semipurpurella* Stph., *E. purpurella* Haw.

Suborder: *Frenata.*

Superfamily Tineoidea; Group Aculeata.

This group of the Tineoidea includes seven families all of which possess minute spicules, aculeæ, on the wing membrane. The significance of these structures has been discussed by Forbes, (1914), and the separation of the Tineoidea (*sens. str.*) into two groups on the basis of these structures is accepted by most microlepidopterists. From a survey of the male genitalia the group seems to be a perfectly natural one, comprised of a series of nearly related families which, with the exception of the Tischeriidæ, are most closely related to the Micropterygidæ. They form a connecting series between the genitalia types of the Micropterygidæ on the one hand and those of the generalized Tineidæ on the other. The group may be distinguished by the following characters: Tegumen small and hood like, usually without an uncus, lateral margins sometimes produced to form two setigerous lobes or processes. Gnathos usually present. Vinculum composed of the ninth sternum, ordinarily large and in the form of a long U or V; apex usually covered by the eighth sternum. Harpes triangular, clavate, or spoon-shaped, sometimes armed with tubercles, or spinose plates. Aedoeagus either a slender chitinized tube or in some species shorter and more heavy; its base is usually enlarged and the ejaculatory duct enters the apex or slightly on the dorsal side. Anellus membranous, often spined and with the free margin cleft or emarginate. Juxta usually absent. Certain modifications of these parts occur in the

different families of the group and will be considered more fully under the following discussion of the special morphology.

Prodoxidæ: (Plate XXIX, Figs. 2 and 4). The genitalia of this family are a modification of the first type described in the Micropterygidæ. The tegumen is reduced and shortened and forms a narrow hood, and is without either an uncus or gnathos; the vinculum is very long and in the form of an acute V; the harpes are spoon-shaped or clavate, and frequently possess chitinous tubercles on the outer margin. The juxta is absent.

Species examined: *Prodoxus quinquepunctella* Chamb., *Tegaticula alba* Zell.

Incurvariidæ: (Plate XXVIII, Fig. 4, and Plate XXIX, Figs 5 and 6). The genitalia of this family resemble those of the preceding quite closely. The tegumen is quite narrow and in some species is provided with a short uncus. The harpes are spoon-shaped or digitate; occasionally the inner margin is divided and forms a short clavus. The anellus in several forms has the free portion divided into lobes and is often spined.

Species examined: *Incurvaria muscalella* F., *I. humilis* Wlsm., *Paraclemensia acerifoliella* Fh., *Isocorypha mediostriatella* Clem.

Adelidæ: (Plate XXVIII, Figs, 5, 7, 8 and 9, and Plate XXIX, Figs. 1 and 3). In structure this family is quite closely related to the preceding, probably having been derived from a Micropterygid ancestor of the type described in group V. In certain respects the genitalia also resembles those of Epimartyria and Eriocrania. The family may be distinguished by the following characters: Tegumen small and hood-like, with or without a gnathos; uncus absent; vinculum very large and usually longer than the eighth sternum under which it lies; it is U or V shaped, often with a medio-ventral spine. Harpes short and triangular, or spoon-shaped, and the inner margin is often adorned with scobinate or spinose plates. These structures anticipate similar ones found in the harpes of the Heliozelidæ. The bases of the inner margins are sometimes fused to a small juxta. Aedoeagus a long, thin, chitinized tube which is sometimes enlarged at the base and armed with a terminal spine. Anellus membranous, often with small spines and a lobed or emarginate, free, portion. The family may be divided into at least three groups based on the shape of the harpes, but insufficient material was at hand to allow a thorough working out of the species on this basis.

Species examined: *Adela viridella* Sc., *A. ridingsella* Clem., *A. septentrionella* Wlsm., *Nematois annæ* Zell., *N. sparsella* Wlk., *Ceromitia Wahlbergi* Zell., *Lampronia* (*Incurvaria*) *prælatella* Schiff., *Nemophora swammerdammella* L.

Nepticulidæ: (Plate XXX, Figs. 1, 3, and 6). The genitalia of this family resemble those of the preceding very closely and have probably been derived from them. The tegumen is short usually with a triangular uncus, and a well chitinized gnathos, composed of two lateral arms and a median plate, or a simple transverse plate. Vinculum large, quadrate, sometimes with the lateral margins expanded, giving it an emarginate appearance. Harpes triangular with the apices acutely

pointed, or clavate; inner basal angles meeting and articulating with the vinculum; hind margins frequently joined by a chitinized transtilla. Aedoeagus extremely large, usually two-thirds as long as the entire genitalia and quite broad. It is often armed with strong spines. Anellus membranous, occasionally armed with spines scattered over the entire surface or in a series around the margin. Margin sometimes produced into spine-like processes. The presence of both gnathos and uncus, the emarginate vinculum, and the broad aedoeagus separates this family from the Adelidæ.

Species examined: *Nepticula slingerlandella* Kearf., *N. rosæfoliella* Clem., *Ectædemia populella* Bsk., *Obrussa ochrefasciella* Chamb., *Glaucolepis saccharalis* Braun., *Trifurcula sp.* (Europe).

Heliozelidæ: (Plate XXX, Figs. 4, 5 and 8). The genitalia of this family resemble those of the genus Ceromitia of the family Adelidæ, from which they have been probably derived. The characteristics are as follows: Tegumen, hoodlike; uncus, absent; gnathos, present; vinculum large, U-shaped, and extending up to the seventh somite; harpes finger-like or spoon-shaped, with a pair of spinose plates on the inner margin, which may be firmly fused to it or elevated on a short process or "petiole." In Heliozela this petiole is long and recurved, thus bringing the plate to one side of the harpe proper and foreshadowing a tendency which is more highly developed in the Opostegidæ. Anellus membranous, usually with a row of recurved spines around the free margin. Aedoeagus long, thin and heavily chitinized, with an eversible termen, which in some species is quite complicated.

Species examined: *Heliozela stannella* Tr., *Antispila isabella* Clem., *Coptodisca splendoriferella* Clem.

Opostegidæ: (Plate XXXI, Figs. 1 and 3). In this family we find a type of genitalia which is quite distinct from any other occurring in the Aculeate Tineoidea and, although it shows some resemblance to the Heliozelidæ, it can hardly be classed as a direct derivation. The characters are as follows: Tegumen, a narrow, transverse hood with two lateral setose papillæ, or a chitinized plate bearing a row of setæ on the margin. Gnathos, when present, quite large and made up of two lateral arms and a median tongue-shaped plate. This structure articulates to the base of the tegumen and swings below the membranous aedoeagus much in the same manner as the suspensorium which was described in the Hepialidæ. The absence of a chitinized aedoeagus and the structure of this peculiarly modified gnathos suggests that it serves as an intromittant organ. When the gnathos is absent the aedoeagus is chitinized and normal in structure. Vinculum narrow and quadrate, or emarginate. Harpes, an extreme modification of the type described in Heliozela. The harpe proper is greatly reduced in size, while the spinose pad is enormously enlarged and bent laterad on its petiole so that it forms a clavate terminal lobe. Anellus membranous. The family may be divided into two subdivisions, the one including those species in which the gnathos is present and the aedoeagus is membranous and the other with the opposite characters.

As a whole the genitalia offer no better suggestion as to the relationships of the family than do the mouth-parts and wing venation. The structure of the harpes suggests that the family might be related to the Heliozelidæ, but all of the other parts are quite dissimilar. The substitution of the gnathos for a chitinized aedoeagus in some species is analogous to the replacement of this structure by a suspensorium in the Hepialidæ, but the modification is evidently developed entirely within the family. The quadrate vinculum which sometimes occurs in the family resembles the same type in the Nepticulidæ, but the emarginate form is much more extreme than any found in Nepticula. Heinrich (1918), from a study of the larval characters of Opostega and allied genera finds its closest affinities with the Nepticulidæ and the Tischeriidæ. From the study of the genitalia just summarized, it will be seen that certain resemblances exist between the Opostegidæ and the Nepticulidæ indicative of relationship, but from the following summary of the Tischeriidæ it will also be seen that there is nothing to indicate even a distant relationship between this family and Opostega. It is unfortunate that Heinrich omitted from his work the Heliozelidæ which seem to be most closely related to Opostega in their genital characters, and the Adelidæ which furnish the intermediate steps from the generalized Aculeates, Incurvariidæ and Prodoxidæ, to these other more highly specialized families.

Species examined: *Opostega nonstrigella* Chamb., *O. auritella* Hb., *O. saliciella* Tr.

Tischeriidæ: (Plate XXX, Figs. 2 and 7). The position of this family is uncertain, for although the wing membrane possesses aculeæ, they are large and not typical. Other structures, (Meyrick, 1895 and 1912), indicate that the family may be related to the genus Bedellia of the Gracilariidæ or Glyphipterygidæ. The genital characters support this latter view, particularly in the shape of the vinculum, the articulation and shape of the harpes and the presence of specialized hair tufts on the eighth sternum. Aside from the resemblance of the spined anellus to the same structure in the Heliozelidæ the family has no genital characters in common with the other Aculeates. The bifed tegumen which occurs in some species slightly resembles the same structure in the Acrolophidæ and Tineidæ, but the bifed condition is carried much further, resulting in two large earlike appendages which have no parallel in any of the forms treated in this paper.

Species examined: *Tischeria tinctoriella* Chamb., *T. marginea* Hw., *T. angusti colella, T. complanella* Hb., *T. malivorella* Clem., *Coptotriche zelleriella* Clem.

Group: *Nonaculeata.*

This group includes all of the remaining families of the Tineiodea about thirty-five of which are represented in North America. Most of these are highly specialized and cannot be regarded as primitive Lepidoptera. The Tineidæ, Acrolepiidæ, Acrolophidæ, Psychidæ, Cossidæ, Bombycidæ, and three families comprising the Eucleoidea possess structural characters in common and with the groups already

described. The special morphology of their genitalia will be described in the following discussion.

Tineidæ: This family forms the basis for practically all of the types of genitalia which occur in the Tineoidea. It may be separated into several fairly well defined divisions which correspond to subfamilies or groups of subfamilies already established on other morphological characters. It is a difficult family to characterize as a whole because these divisions are the result of several lines of specialization, which have culminated in widely separated types. The most satisfactory idea of the genitalia of the family may be obtained by a discussion of these types within their respective divisions.

Division I: (Plate XXXI, Figs. 2 and 4–9). This division contains those Tineids commonly classed under the subfamilies Eriocottinæ, (=Xysmatadominæ), and Crinopteryginæ, and is characterized as follows: Tegumen very large and hood-like, probably made up of the ninth and tenth terga although there is no distinct suture between them, posterior margin emarginate or deeply bifed. Uncus not distinct although the posterior margin of the tenth tergite is sometimes produced and forms a triangular lobe, i. e. Timæa. The gnathos consists of two chitinized arms and a median plate which may be membranous or chitinized. Vinculum U or V shaped, with or without a saccus. The form of the saccus varies from a shallow pocket to a long keel-like spur. The harpes are broad and spoon shaped, either undivided with a small spur near the base of the outer margin, (Eriocottis), or divided into a distinct cucullus and sacculus, (i. e. Narycia.) The Transtilla is well developed in some species and forms a bridge behind the ædœagus. The anellus is usually membranous, sometimes with short spines, and the juxta, when developed forms a small chitinized plate which may bear a pair of lateral lobes. The ædœagus varies greatly in size and degree of chitinization, but is usually a linear tube without armature.

The origin of this type of genitalia is difficult to trace for it seems somewhat isolated from the Jugo-frenata and Aculeata. From the characters offered by the European genera, Crinopteryx and Eriocottis and the Australian genera Mallobathra, Mesopherna, and Timæa, it seems most logical to regard it as a derivation of the Micropterygidæ, probably from group I. The large tegumen composed of the ninth and tenth terga, the simple U- or V-shaped vinculum, the spoon shaped harpes and the linear ædœagus are all structures which could be derived from a generalized form of genitalia such as already described in Sabatinca.

The more highly specialized members of this first group, i. e., Rhodobates, Apreta, and Dryotopasta serve as a basic type from which may be derived the genitalia of the Acrolophidæ, while the generalized type represented by Eriocottis, etc., are closely related to the second division of the Tineidæ through the genus Solenobia.

Division II: (Plate XXXII, Figs 1–7, and Plate XXXIII, Fig. 5). This division includes the sub-families Telæporiinæ, Teichobiinæ, and certain Tineid genera placed by some authors in the Psychidæ. The

group forms a transition on one side between the Eriocottinæ and the Psychidæ in which all of the intermediate steps in genitalia development have been preserved, and on the other between the Eriocottinæ and the Tineidæ in which only a few intermediate forms have been preserved. The characters of the group are difficult to define because of the wide variation. The more generalized forms such as Solenobia resemble Eriocottis and Crinopteryx, but the more specialized ones are quite distinct. The tegumen is large and hoodlike in the generalized forms, but tends to become narrow in the forms more closely related to the Psychidæ. It is usually without an uncus or gnathos although the latter is sometimes present. The vinculum is V-shaped moderately large and usually possesses a short, blunt, or obtuse saccus. The harpes are either spoon shaped with a short projection near the base of the outer margin, or completely divided. The juxta is well developed in most species and is in the form of a large plate in front of or surrounding the ædœagus. Its lateral margins frequently bear a pair of hairy lobes. The ædœagus is usually large, especially in those forms resembling the Psychidæ, well chitinized and with little armature.

Division III: This division contains most of the species placed by authors in the Tineinæ with the exception of a few which have already been included under Divisions I and II. Two quite distinct types of genitalia occur in the group, which appear to be the result of two diverging lines of specialization from a form similar to Teichobia or Diachorisia. Both of these types occur in the genus Tinea and will be referred to as subdivisions A and B.

Subdivision "A": (Plate XXXIII, Fig. 3, and Plate XXXIV, Figs. 1, 2, 4, 5 and 7). In this group is included all of the Tineidæ in which the saccus is well developed, i. e., The genotype of Tinea, most of the North American and European species of the genus, and closely allied genera such as Monopis and Tineola. In the more typical of the group the uncus, gnathos, and saccus are all extremely well developed, but in reduced forms such as Oencœ and Homostinea the entire tegumen and its armature is greatly abbreviated. The Australian genus Mœrarchis is intermediate between the two subdivisions but cannot be considered as a transitional form because this separation on the basis of the presence or absence of a saccus is hardly a natural one. It is possible that such reduced forms as Ischnosia, Meesia, etc., which I have placed in the second subdivision may have lost the saccus through reduction just as they have the uncus and gnathos. These genera are exceedingly difficult to place due to the absence of these structures. Isocorypha which has been placed by some authors among the genera included in this group bears more resemblance to the Incurvariidæ, especially Paraclemensia, and is placed in that family. The ædœagus in this subdivision is usually linear, quite long, and needlelike. The harpes are usually spoon shaped or finger-like.

Subdivision "B": (Plate XXXIV, Figs. 3, 6, 9 and 10). As already mentioned this subdivision differs from the former in the absence of the saccus and in having the vinculum enlarged, forming a rectangular,

U-shaped, or emarginate plate. The uncus and gnathos are absent or reduced and the former is sometimes replaced by socii. The harpes are very irregular, often with spines and processes. The ædœagus is usually large at the base and acutely pointed at the apex and often abruptly curved. Homosetia which is placed in this subdivision closely resembles Diachorisia and Ateliotum of Division II. It has been very difficult to ascertain the positions of these three genera from the genitalia because they are somewhat intermediate in their structure between Divisions II and III.

Division IV: (Plate XXXIII, Figs. 1, 2, 4 and 6). This division includes the two genera Amydria and Scardia, which are usually placed in the Tineinæ. Their genitalia resemble those of the Acrolophidæ, and they were probably derived along with this family from a form similar to Alavona, Dryotopasta or Rhodobates of Division I. They are characterized by having a bifid or emarginate uncus, a U-shaped vinculum, an incomplete or rudimentary gnathos, and emarginate or divided harpes. These are large and irregular and are composed of two or three lobes, the inner one sometimes forming a hook or process. The anellus is small and sometimes armed with short spines; and the juxta is well developed. In Scardia it forms a plate which surrounds the ædœagus. The ædœagus is large and linear, slightly dilated at the base and often armed with small spines or teeth at the termen; vesica, prominent. Most of the species of Scardia answer the foregoing description, but Amydria is divided into two distinct groups. The first of these represented by the genotype *effrentella* Clem. (Plate XXXIII, Fig. 1) possesses irregular harpes and a curved, acutely pointed ædœagus, and the second, represented by *margoricella* Dtz. (Plate XXXIII, Fig. 6) has simple spoon shaped harpes and a linear ædœagus. The species of Tineidæ which were examined are listed below according to the divisions just described.

Division I: *Crinopteryx familiella* Peyr. *Eriocottis pyrocoma* Meyr., *E. andalusiella* Z., *E. fuscanella* Z., *Mallobathra cratæa* Myer., *Timæa biviltatella* Wlk., *Mesopherna palustris* Meyr., *Alavona barbarella, Rœslerstammia pronubella* Schiff., *R. erxlabenella* F., *Lypusa maurella* F., *Narycia saxosa* Meyr., *N. heliochares* Meyr., *N. trifasciata* Wlk., *Lepidoscia palleuca* Meyr., *Rhodobates lævigatellus* H. S., *R. pallipalpellus* Rb., *Dryotopasta yumælla* Kearf., *Apreta paradoxella* Dietz.

Division II:

Telæporiinæ: *Solenobia manii* Z., *S. walshella* Clem., *Telæporia tabulosa* Ritz., *Diplodoma marginapuncta* Stph., *Melasina lugubris* Hb., *Kearfottia albifasciella* Fern., *Dissoctona granigerella* St., *Dysmasia parietariella* H. S., *Euplocamus delagrangei* Rag., *Mymecozela danubiella* Mn.

Teichobiinæ: *Diachorisia vilatella* Clem., *Teichobia verhuellella* Stt., *Ateliotium hungaricellum* Z.

Division III: Subdivision "A": *Mœrarchis australasiella* Zell., *M. inconcisella* Wlk., *Tinea fuscipunctella* Hw., *T. pellionella* L., *Tineola bisselliella* Hum., *Trichophaga abruptella* Woll., *Monopis rusticella* Hbn., *M. dorsistrigella* Clem., *M. crocicapitella* Clem., *M. unibractella* Wlk., *Xylesthia pruniramiella* Clem., *Setomorpha insectella* Fab., *Oenoe hybromella* Clem., *Homostinea curviliniella* Dtz.

Subdivision "B": *Homosetia miscecristatella* Chamb., *Ischnosia boreonella* Mill., *Tinea purella* Wlk., *T. xystidophora* Meyr., *T. misella* Zell., *Meesia argentimacuella* H. S., *M. vinculella* H. S.

Division IV: *Amydria effrenatella* Clem., *A. margoricella* Dtz., *Scardia boleti* F., *S. fiskeella* Busck., *S. coloradella* Dtz.

Acrolepiidæ: (Plate XXIV, Fig. 8). From an examination of the genitalia of the North American species of the genus Acrolepia and the European genus Roeslerstammia which has also been placed in the family by some authors it seems very doubtful if these genera are to be regarded as separate from the Tineidæ. Roeslerstammia is quite similar to Eriocottis and the genera forming Division I of the Tineidæ and has been placed there. Acrolepia resembles the reduced Tineids, Ischnosia and Meesia, and unless further examination of the European species reveals a different type of genitalia it may be regarded as one of the saccus-bearing Tineidæ. The family shows no close affinity with the Plutellidæ, where some authors have placed them.

Species examined: *Acrolepia incertella* Chamb. *Ræslerstammia pronubella* Schiff. *R. erxlabenella*, F.

Acrolophidæ: (Plate XXXV, Figs. 1–7). The characteristics for the genitalia of this family are much the same as in Division IV of the Tineidæ. The uncus is usually bifid, but the two portions are often approximated or fused. The harpes are spoon-shaped and when divided form a spoon-shaped or finger-like cucullus and a clavate or pointed sacculus. The aedoeagus is large, slightly bulb-like at the base, and has a large eversible vesica which bears one or more strong spines (cornuti); occasionally the termen is acutely pointed. The anellus is unchitinized, but sometimes armed with spines; the juxta is rudimentary or absent. The North American species which were described under a series of new genera by Walsingham (1887), were later combined under the original genus Acrolophus by Barnes and McDunnough, (1917). From an examination of the genitalia this seems advisable. Anaphora and Acrolophus show no difference in genitalia, both being subject to the same variations, and none of the remainder of Walsingham's genera which were examined appear at all distinct. In fact, Walsingham admits as much in his revision when he says that, "the sexual appendages on the ultimate segments of the bodies of the males have been found reliable in separating the species, although certainly not uniform throughout the genera." As already mentioned, the type of genitalia in this family is nearest Division IV of the Tineidæ, both of which have been derived from the first division of the latter family. In fact, it has been difficult to place such intermediate forms as Apreta and Dryotopasta, and if it were not for the characters furnished by the wing venation and mouth-parts of the Acrolophidæ the family could easily be regarded as a fifth group of the Tineidæ.

Species examined: *Acrolophus* (*Pseudanaphora*) *arcanellus* Clem., *A.* (*Felderia*) *filicornis* Wlsm., *A.* (*Ortholophus*) *variabilis* Wlsm., *A.* (*Anaphora*) *popeanellus* Clem., *A.* (*Atopocera*) *barnesi* Dyar., *A. plumifrontellus* Clem., *A.* (*Hypoclopus*) *mortipennellus* Grt., *A.* (*Eulepiste*) *kearfotii* Dyar., *A.* (*Neolophus*) *punctellus* Bsk., *A. sp.* (Panama); *Amisthus gigas* (Peru).

In the Figures illustrating the genitalia of this family, *Acrolophus mortipenellus* (Plate XXXV, Fig. 2) serves to illustrate the genotype for both Anaphora and Hypoclopus in which I see no difference; and *A. plumifrontellus* (Plate XXXV, Fig. 7) shows the type in those species of Acrolophus, which have the harpes divided and the sacculus produced

to form an acute clavus. Most of the species examined belong to the first type.

Psychidæ: (Plate XXXVI, Figs 1, 2, 3 and 6). The genitalia of this family, as already mentioned, are a modification of the type described in the Telaeporiinæ, (Tineidæ Division II), the genera Melasina, Dissoctena, and Dysmasia forming the intermediate forms between the typical Telaeporrids and such types as Chalia and Eurycyttarus of the Psychidæ. The Australian genus Ellasoptila also represent an intermediate type, but seems to constitute an independent line of genital specialization which has preserved many tendencies in common with the Acrolophidæ and Cossidæ. Strand (1912), suggests that the family is not monophyletic, but from an examination of species from all parts of the world we find it is a very homogeneous one, Elassoptila being the only exception. Since the Psychidæ have originated from a generalized Tineid ancestor, as have also the Cossidæ, it is not surprising to find in some species tendencies in common with the latter. The characters of the family are as follows: Tegumen elongate and narrow, forming a dorsal hood, which is sometimes emarginate at the apex. Vinculum long and narrow, with an extremely long saccus. Harpes very small, emarginate or bifid at the apex, often forming a short sacculus. Aedoeagus very large and long, sometimes with a blub-like base and funnel-shaped termen. Juxta chitinized and fused with the harpes. Sometimes the vinculum and transtilla fuse laterally and form a ring around the aedoeagus. Eighth sternum heavily chitinized and forming a large plate with its anterior lateral margins produced to form two large lobes. The extreme elongation of the genitalia and the modification of the eighth sternum separates the family from most of the Telaeporiinæ. In some of the transitional forms, however, i. e., Dysmasia and Kearfottia, the last character does not apply.

Species examined: *Elassoptila mixroxutha* Turn. (Austr.); *Eurycyttarus confederata* Grt., *Chalia rileyi* Heyl., *Platæceticus gloveri* Pack., *Oiketicus omnivorus* Wlk. (N. Z.); *Thyridopteryx ephemeræformis* Haw., *Eumeta moddermanni* Heyl. (Africa); *Clania ignobilis* (Australia).

Cossidæ: (Plate XXXVI, Figs. 4, 5, 7, 8 and 9). The genitalia of this family combine tendencies from the Tineoidea and Hepialidæ, but show closest affinities with the Acrolophidæ. The tegumen is large and hood-like, with a simple or bifid uncus; the gnathos is usually present, although the median portion is poorly developed. The vinculum is small U or V-shaped and usually possesses a short saccus. The harpes are large, spoon-shaped and simple. The aedoeagus is large, well chitinized and has a broad membranous termen; occasionally it is acutely pointed. The anellus is membranous, often with longitudinal plicæ; the juxta is large, chitinized and has a pair of lateral processes. The bases of the harpes, the juxta, and the aedoeagus are closely associated or fused, suggesting a similar relation of these parts in the Hepialidæ. The simple uncus in some species is suggestive of the dorsal processes which occur in some Hepialids, Gorgopis. The prevailing simplicity of the harpes aedoeagus and vinculum indicates a

tendency on the part of this family to retain more generalized characters than those described in the higher Tineidæ and Acrolophidæ. In the Figures illustrating this family, *Cossula magnifica* (Plate XXXVI, Fig. 7) presents a highly specialized type, in which the vinculum and anellus are reduced and the uncus inclined ventrad closely approximating the gnathos.

Species examined: *Givira mucidus* H. Edw., *G. cleopatra* B. and McD., *G. ethela* N. and D.; *Zeuzera pyrina* L., *Z. asylas*, *Z. multistrigata* Mr., *Eudoxyla strix.*, *Hamilcara ramuscula* Dy., *Cossula magnifica* Stkr., *Fania nanus* Stkr., *Comadia bertholdi* Grt., *C. henrici* Grt., *C. engelhardti* B. and Benj., *C. dolli* B. and Benj., *C. subterminata* B. and Benj., *Acossus orc* Stkr., *Prionoxystus robiniæ* Peck.

Superfamily *Eucleoidea.*

Limacodidæ (Cochlididæ and Eucleidæ): (Plate XXXVII, Figs. 1–7). The genitalia of this family resemble those of the Cossidæ. The tegumen is much like that described for the Cossidæ, although the uncus is usually longer, more acutely pointed, and the arms of the gnathos are fused to a central plate. The vinculum is usually quite long and without a saccus. In *Cania bandura* (Plate XXXVII, Fig. 1), however, the vinculum is narrow and has a broad, short saccus. The harpes are spoon-shaped, either divided into a cucullus and sacculus or with a short spine on the outer margin as in the Eriocottinæ. The anellus is usually heavily spined or occasionally completely chitinized, forming a funnel around the aedoeagus. The juxta is similar to that in the Eriocottinæ. The aedoeagus is quite long, with a large heavily chitinized, bulb-like base; the termen is sometimes armed with cornuti. The origin of the genitalia appears to be from a very generalized Tineid ancestor and the family has retained a majority of Tineid tendencies. The Figures of *Cochlidion avellana* (Plate XXXVII, Fig. 2) and *Euclea delphinii* (Plate XXXVII, Fig. 7) illustrate the type which prevails in the North American and European species, while Heterogenea (Fig. 4), Microleon (Fig. 6), Miresa (Fig. 3), Setora (Fig. 5), and Cania (Fig. 1) illustrate various lines of modification.

Species examined: *Cochlidion avellana* L. (=*limacodes* Hufn.); *C. christophi* Græs., *Limacodes biguttata* Pack., *L. rectilinea* G. and R., *Euclea delphinii* Bdv., *E. delphini, quercicola* H. S., *E. delphinii*, form *pænulata* Clem., *Heterogenea asella* Schiff., *Adoneta spinuloides* H. S., *Lithacodes fasciola* H. S., *Packardia geminata* H. S., *Microleon longipalpis* Butl., *Doratifera vulnerans* Lew., *Neæra* (Parasa) *dispar* (Java)., *Setora nitens* (Java)., *Susica corones* Fab., *Miresa flavescens* Wlk., *Cania bandura* Wlk. (Sumatra).

Megalopygidæ: (Plate XXXVIII, Figs. 1, 2, 5 and 7). The representatives of this family present two widely separated lines of genital specialization and as the author has been unable to examine material from localities other than in North America, the family relationships have been difficult to ascertain. Judging from the material at hand they are derived from a primitive Jugo-frenate type, and have preserved certain Hepialid characters. The group may be separated into two divisions, the first containing the genera Norape and Trosia (Figs. 7 and 2), which closely resemble the Hepialidæ, and the second containing Megalopyge and Lagoa (Fig. 1) which show little resemblance

to any other Lepidoptera except possibly the Dalceridæ (Fig. 3). The first is characterized by having a short tegumen, a rudimentary uncus and gnathos, and a small V-shaped vinculum, which is well chitinized near the median line, but membranous at the lateral angles. The harpes are divided into a spoon-shaped cucullus and a clavate or triangular sacculus. The cucullus is articulated to the tegumen, while the sacculus is solidly fused with the juxta; in N. tener (Fig. 7) practically the entire harp is fastened to the juxta, only the costal angle being articulated to the tegumen. The anellus is large, usually heavily chitinized and the juxta forms a plate occupying the entire meso-ventral portion of the genitalia. The aedoeagus is large, heavily chitinized, usually armed with an apical spine and has at least one spine on the vesica. The second group is characterized by a complete separation of the cucullus and sacculus of the harpes, so that the former are attached to the tegumen near the uncus and the latter retain their articulation with the juxta. The juxta is often greatly reduced and fused with the vinculum. The uncus is placed on a large basal plate which is entirely separated from the tegumen by membrane. The tegumen is enlarged and forms a broad hood. The aedoeagus is much like that in the first group except that the vesica is armed with a number of small cornuti. The fusion of the harpes with the juxta and the shape of the vinculum and tegumen in the first group places this series very near the Hepialidæ and the second group may be considered as a development of the first. Since these same Hepialid tendencies are shared by the Lacosomidæ and Bombycidæ, it is very likely that these two families and the Megalopygidæ represent the remnants of a broken series which once connected the Hepialidæ and the Bombycidæ.

Species examined: *Norape tener* Druce, *N. virgo* Butl., *N. ovina* Sepp., *Megalopyge opercularis* A. and S., *M. bissessa* Dyar., *M. heteropuncta* B. and McD., *Lagoa crispata* Pack., *L. pyxidifera* A. and S.

Dalceridæ: (Plate XXXVIII, Fig. 3). This small family, which is represented in North America by a single species, exhibits unique genital characters. The harpes are greatly reduced and the saccus is fused with the anellus and vinculum on the meso-ventral line, while the cucullus is indistinguishably fused with the tegumen, forming a pair of dorsal ear-like lobes. The gnathos is represented by a pair of triangular setose lobes, armed with a serrate ridge. The vinculum is small and bears a long saccus of the type similar to that described in the Tineidæ. The aedoeagus is long and lightly chitinized. The status of the family is difficult to determine from the genitalia, but it seems to be most closely related to the Megalopygidæ, but has preserved a Tineid-like vinculum, saccus and aedoeagus.

Species examined: *Dalcerides ingenita* Hy. Edw.

Superfamily *Bombycoidea*.

The families of this group, which show closest genital affinities with the primitive Lepidoptera, are the Lacosomidæ and Bombycidæ. As already mentioned, these families have the harpes articulated or fused with the juxta, a character already noted in the Hepialidæ, Cossidæ,

Megalopygidæ, et al. The Bombycidæ have the vinculum and saccus well developed, as in the Tineoidea, while the eighth sternum is chitinized resembling that of the Hepialidæ. The remaining characters of the group are not of particular importance from the viewpoint of this paper and a complete survey is not attempted. An idea of the two main types of genitalia may be formed from the Figures of *Lacosoma chirodota* Grt. (Plate XXXVIII, Fig. 6), and *Bombys mori* L. (Plate XXXVIII, Fig. 4).

CONCLUDING REMARKS ON THE RELATIONSHIPS OF THE PRIMITIVE LEPIDOPTERA AS DETERMINED FROM A STUDY OF THE MALE GENITALIA.

In any attempt to determine the phylogenetic relationships of a group of animals the entire structure of the body as well as the biology should be considered. It would be entirely beyond the scope of this paper to do this for the primitive Lepidoptera, but an examination of the results obtained from a study of their genitalia, with the additional consideration of opinions held by workers in other phases of their anatomy and biology, will contribute to the sum total of our knowledge concerning the phylogeny of these interesting insects.

From our comparison of the structure of the male genitalia in the generalized representatives of various insect orders with those of the Lepidoptera, it was seen that the parts comprising the male genitalia can be homologized with little difficulty. Zander's conception of a common plan of structure for the Trichoptera, Hymenoptera and Lepidoptera may be extended to the Neuroptera and Orthoptera and to insects in general. The type of genitalia in all of these orders is quite similar and may be traced to tendencies developed in one of the most primitive orders of winged insects, i. e., the Ephemerida.

From a study of the wing venation, mouth-parts, and other characters in the primitive Lepidoptera, Packard (1895), Meyrick, Busck (1914), et al., have concluded that the Lepidoptera have arisen from Trichoptera-like ancestors, i. e., possibly from the Rhyacophilidæ through the Micropterygidæ. Quite apart from these investigations Zander and Cholodkovsky have shown that close resemblances exist between the external and internal genitalia of the Molannidæ and Hepialidæ on one hand and the Rhyacophilidæ and Micropterygidæ, and the Sericostomatidæ and the Tineidæ on the other. From our own investigations we have seen that the development of the different

types of genitalia in the primitive Lepidoptera is paralleled by a development of similar ones in the Trichoptera, certain families in each order bearing a striking resemblance to each other. Two lines of development are discernible, the one represented by the Jugata (Hepialidæ), which finds its parallel in the Lepto-

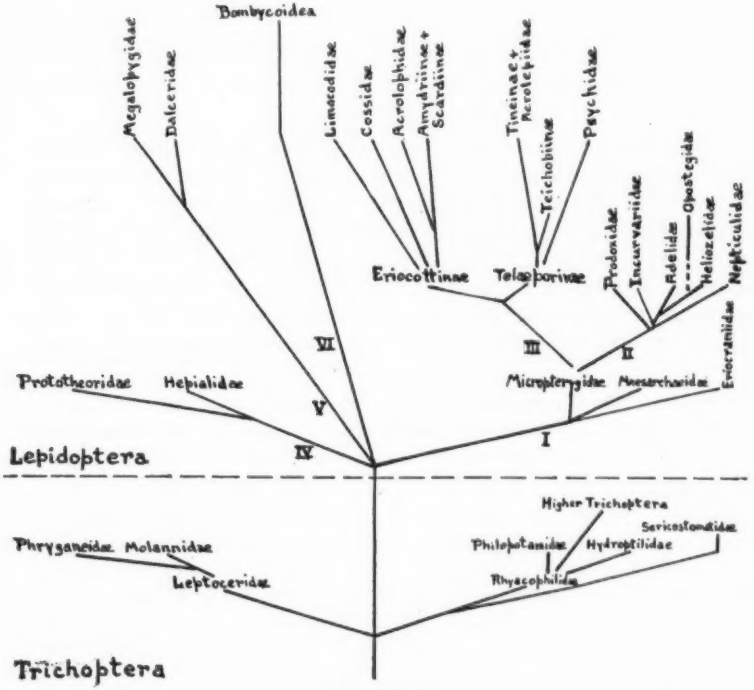

FIGURE X.

Phylogenetic Tree Illustrating the Relationships of the Families of Primitive Lepidoptera as Ascertained from a Study of Their Male Genitalia.

ceridæ, Molannidæ and Phryganeidæ, and the second represented by the Jugo-frenata and Tineoidea and finding its parallel in the Rhyacophilidæ, Philopotamidæ, Hydroptilidæ and Sericostomatidæ.

Consequently in seeking for a generalized type of genitalia from which the various lines of specialization in the primitive Lepidoptera and Trichoptera have been derived, we must expect

to find characters intermediate between these two lines of development, a type, however, which we can hardly realize in any living insect of today. The nearest approach to such a form is most probably in Mnesarchaea and Sabatinca of the Lepidoptera and in Leptocerus and Molanna of the Trichoptera. In these we find the following generalized characters: A relatively simple tegumen, composed of the fused ninth and tenth terga, which is without a distinct uncus or gnathos; a vinculum composed of the ninth sternum which has retained its normal shape and size; simple harpes which are articulated to the meso-ventral surface of the vinculum by a membranous or lightly chitinized juxta; a simple tube-like, membranous, or lightly chitinized aedoeagus. All of these characters exist in a slightly modified degree in the two generalized forms mentioned.

From such a type we may conceive of the Trichoptera as developing in two diverging lines, the one culminating in the present day Leptoceridæ, and the other in the Rhyacophilidæ. From these two branches have been derived the remaining families of our modern Trichoptera. Slightly higher in the scale, but from a similar generalized type the Lepidoptera have arisen as a dichotomous stem, one branch of which has paralleled the Molannid branch of the Trichoptera, resulting in the Hepialidæ and Prototheoridæ and the other paralleling the Rhyacophilidæ, resulting in the Micropterygidæ and Mnesarchaeidæ. The accompanying phylogenetic tree (Text Fig. X), illustrates the relations just described. Four main groups of Lepidoptera yet remain to be accounted for, i. e., the Aculeate and Non-aculeate Tineoidea, the Eucleoidea, and the Bombycoidea. The first of these, the Aculeate Tineoidea, have their closest affinities with the Jugo-frenate, especially the Micropterygidæ, and are figured arising from these forms on a common stem. The non-aculeate Tineoidea are clearly related to the aculeate series and to the Jugo-frenata through the subfamilies Eriocottinæ and Crinopteryginæ and this relationship is indicated by the origin of the stem from which they diverge. The Psychidæ are also related to this series through the Telaeporiinæ. The Cossidæ, which resemble the Acrolophidæ more closely than any other family, are also included here, along with the Limacodidæ.

The Megalopygidæ and Dalceridæ have many characters in common with both Jugate Lepidoptera and Tineoidea, but show little direct connection with either through transitional forms. Consequently, they are derived from the point of common origin of the Hepialidæ and Tineoidea and the Megalopygidæ, which seem most closely allied to the Hepialidæ, through the genus Norape, are inclined toward the Jugate stem. The Bombycoidea, which are quite intermediate in their genitalia characters, are tentatively placed in the central portion of the tree, thus showing their relations to both sides.

In constructing the phylogenetic tree the rules laid down by Busck (1909) have been followed. The main branches I to VI, represent the larger groups or super-families, into which the primitive Lepidoptera have been divided in our previous discussion. All of the families or sub-families which originate from one of these main branches are to be regarded as separate systematic entities having a common ancestor. Their origins are indicated by the position of the bases of their respective branches and their degrees of specialization by their vertical elevations in the tree. Thus the Prodoxidæ, Incurvariidæ, and Adelidæ are derived from a common ancestor and have attained the same degree of specialization along slightly divergent lines. The Heliozelidæ and Opostegidæ, although likewise derived from the same aculeate stock, have surpassed these other families and attained a much higher degree of specialization. The Crinopteryginæ and Eriocottinæ, on the other hand, have attained the same relative degree of specialization as the generalized Aculeata (Prodoxidæ and Incurvariidæ), which they closely resemble in certain genital characters, but they have had their origin in more recent times from a non-aculeate ancestor and have attained these similar characters along entirely separate lines.

Explanation of Figures.

The Figures illustrating the forms described in this discussion have been drawn from slides of the genitalia which were softened in potassium hydroxide, cleared in carbon xylol, and mounted in Canada balsam. The outline was first traced from the slide by using a projection lantern with a microscope attachment, thus insuring a correct depiction of the shape and position of the structures. The details were then added from a study of the

parts under the high power of a compound microscope. No attempt was made to draw the Figures to a definite scale, for the great variation in size, often within the same family, made this impractical. If such a practice had been followed, the genitalia of the largest species would require a full page cut and the smallest would be scarcely large enough for satisfactory reproducing. Consequently, all of the Figures were made of sufficient size to best show the structure of their component parts. Unless specified otherwise in an accompanying legend, the Figures depict the ventral aspects of the genitalia, and the harpes are opened laterad to reveal the inner structures which would be obscured by them. The aedoeagus also is frequently removed in order to obtain a better view of it and the parts which it overlies.

The custom which most taxonomists use of accompanying the Figure with the name of the species has been followed, and in order to make this work useful to the taxonomist as well as to the comparative morphologists the genotype has been figured wherever possible. Whenever the type of the genus on which an important family is based was not available for study a large series of species were examined and the most typical one figured. When two or more distinct lines of specialization were observed to occur in a family or genus, Figures illustrating these types were included.

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EXPLANATION OF PLATES.

PLATE XXV.

Hepialidæ and Micropterygidæ.

1. *Hepialus lupulinus* L.
2. *Perrissectis australasiæ* Don. Right harpe.
3. *Hepialus humuli* L.
4. *Oxycanus (Porina) fuscomaculatus* Walk.
5. *Hepialus hectoides* Boisd. Right harpe.
6. *Trictena labyrinthica* Don.
7. *Phassus metellus* Druce. Eighth tergite included.
8. *Micropteryx rablensis* Zell. Latus of tegumen and ædœagus.
9. *Porina novæ-zealandiæ* Walk.

PLATE XXVI.

Hepialidæ, Prototheoridæ and Micropterygidæ.

1. *Gorgopis libania* Stoll.
2. *Hepialus (Charagia) eximius* Scott. Right harpe.
3. *Micropteryx thunbergella* F.
4. *Prototheora petrosema* Meyr.
5. *Micropteryx Rothenbachii* Frey. Latus of tegumen.
6. *Palpifer sexnotatus* Moore.
7. *Micropteryx aruncella* Sc. Lateral view of right side.
8. *Oncoperalintricata* Walk.

PLATE XXVII.

Micropterygidæ and Eriocraniidæ.

1. *Sabatinca calliplaca* Meyr. Ventro-lateral view of right side.
2. *Epimartyria auricrinella* Wlsm. Aedœagus at left.
3. *Sabatinca chrysargyra* Meyr. Aedœagus at right.
4. *Sabatinca incongruella* Walk. Ventro-lateral view of right side.
5. *Micropteryx calthella* L. Lateral view of left side.
6. *Eriocrania semipurpurella* Stph. Lateral view of left side.
7. *Sabatinca doroxena* Meyr. Lateral view of left side; ædœagus at right.
8. *Sabatinca eodora* Meyr. Aedœagus at right.

PLATE XXVIII.

Eriocraniidæ, Mnesarchæidæ and Adelidæ.

1. *Mnemonica subpurpurella* Haw. *fastuosella* Zell.
2. *Eriocrania unimaculella* Zett.
3. *Mnesarchæa loxoscia* Meyr.
4. *Isocorypha mediostriatella* Clem. Eighth somite included.
5. *Adela viridella* Sc.
6. *Mnesarchæa hamadelpha* Meyr.
7. *Adela septentrionella* Wlsm.
8. *Nemophora swammerdamella* L.
9. *Ceromitia Wahlbergi* Zell.

PLATE XXIV.

Adelidæ, Incurvariidæ and Prodoxidæ.

1. *Lampronia (Incurvaria) prælatella* Schiff. Left harpe reversed.
2. *Tegaticula alba* Zell.
3. *Nematois annæ* Zell.
4. *Prodoxus quinquepunctellus* Chamb.
5. *Paraclemensia acerifoliella* Fitch.
6. *Incurvaria muscalella* F.

PLATE XXX.

Nepticulidæ, Heliozelidæ and Tischeriidæ.

1. *Obrussa ochrefasciella* Chamb.
2. *Coptotriche zelleriella* Clem.
3. *Ectædemia populella* Bsk.
4. *Antispila isabella* Clem.
5. *Coptodisca splendoriferella* Clem.
6. *Nepticula slingerlandella* Kearf.
7. *Tischeria malifoliella* Clem.
8. *Heliozela stannella* F. R.

PLATE XXXI.

Opostegidæ and Tineidæ.

1. *Opostega nonstrigella* Chamb.
2. *Narycia saxosa* Meyr. Right harpe.
3. *Opostega salaciella* Tr.
4. *Apreta paradoxella* Dtz. Aedœagus at right.
5. *Narycia* (*Xysmatodoma*) *heoliochares* Meyr.
6. *Dyotopasta yumælla* Kearf.
7. *Eriocottis fuscanella* Z.
8. *Lypusa maurella* F.
9. *Rhodobates pallipalpellus* Rb.

PLATE XXXII.

Tineidæ.

1. *Euplocamus delagrangei* Rag.
2. *Diachorisia vilatella* Clem.
3. *Ateliotum hungaricellum* Zell.
4. *Melasina lugubris* Hb.
5. *Telæporia tabulosa* Ritz.
6. *Solenobia walshella* Clem.
7. *Teichobia verhuellella* Stt.

PLATE XXXIII.

Tineidæ.

1. *Amydria effrenatella* Clem.
2. *Scardia boleti* F.
3. *Setomorpha insectella* F. Eighth sternite in part included.
4. *Scardia coloradella* Dtz.
5. *Kearfottia albifasciella* Fern. Eighth sternite included.
6. *Amydria margoricella* Dtz.

PLATE XXXIV.

Tineidæ and Acrolepiidæ.

1. *Monopis dorsistrigella* Clem.
2. *Xylesthia pruniramiella* Clem.
3. *Homosetia miscecristatella* Zell.
4. *Mærarchis australasiella* Zell.
5. *Oenæ hybromella* Clem.
6. *Tinea xystidophora* Meyr.
7. *Tinea pellionella* L.
8. *Acrolepia incertella* Chamb.
9. *Tinea misella* Zell.
10. *Meesia vinculella* H. S.

PLATE XXXV.

Acrolophidæ.

1. *Acrolophus* (*Neolophus*) *punctellus* Bsk. Aedœagus.
2. *Acrolophus* (*Hypoclopus*) *mortipennellus* Grt.
3. *Acrolophus* (*Eulepiste*) *kearfotti* Dyar. Aedœagus.
4. *Acrolophus* (*Ortholophus*) *variabilis* Wlsm.
5. *Acrolophus* (*Eulepiste*) *maculifer* Wlsm. Aedœagus.
6. *Amisthus gigas* (Peru).
7. *Acrolophus plumifrontellus* Clem.

PLATE XXXVI.

Psychidæ and Cossidæ.

1. *Thyridopteryx ephemeræformis* Haw. Eighth sternite included.
2. *Chalia rileyi* Heyl.
3. *Eurycyttarus confederata* Grt. Eighth sternite included.
4. *Givira cleopatra* B. & McD. Tegumen and uncus.
5. *Eudoxyla strix* (Australia). Aedœagus at right.
6. *Elassoptila microxutha* Turn.
7. *Cossula magnifica* Stkr.
8. *Givira mucidus* H. Edw.
9. *Zeuzera multistrigata* Mr. Tegumen, uncus, gnathos and juxta.

PLATE XXXVII.

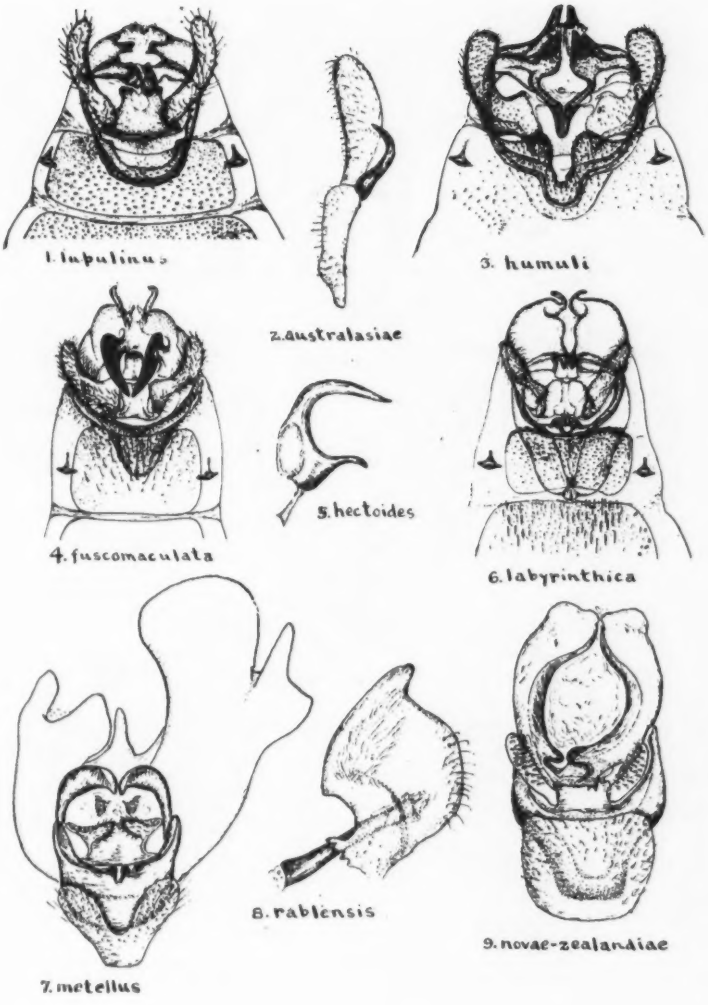
Limacodidæ.

1. *Cania bandura* Wlk.
2. *Cochlidion avellana* L.
3. *Miresa flavescens* Wlk.
4. *Heterogenea asella* Schiff.
5. *Setora nitens* Wlk.
6. *Microleon longipalpis* Butl.
7. *Euclea delphinii* Bdv. Aedœagus at right; right harpe cut off.

PLATE XXXVIII.

Megalopygidæ, Dalceridæ, Bombycidæ and Lacosomidæ.

1. *Megalopyge opercularis* A. & S. Aedœagus at left.
2. *Trosia obsolescens* Dyar.
3. *Dalcerides ingenita* H. Edw.
4. *Bombyx mori* L. Eighth sternite included.
5. *Norape ovina* Sepp. Aedœagus.
6. *Lacosoma chiridota* Grt.
7. *Norape tener* Druce.


1. lupulinus
2. australasiae
3. humuli
4. fuscomaculata
5. hectoides
6. labyrinthica
7. metellus
8. rablensis
9. novae-zealandiae

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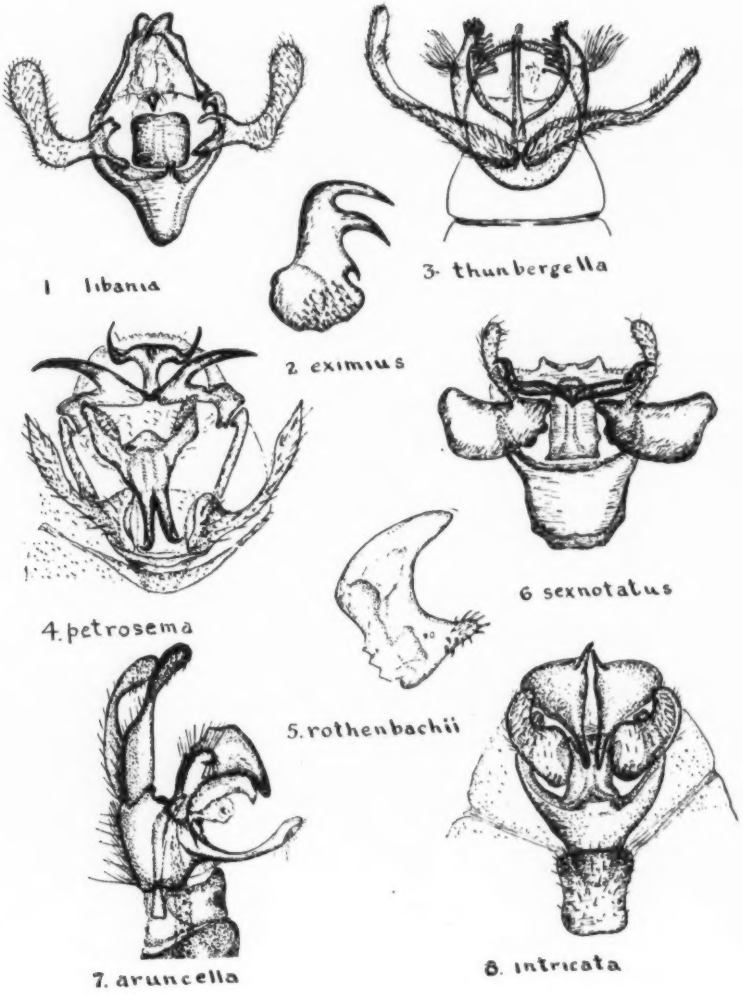
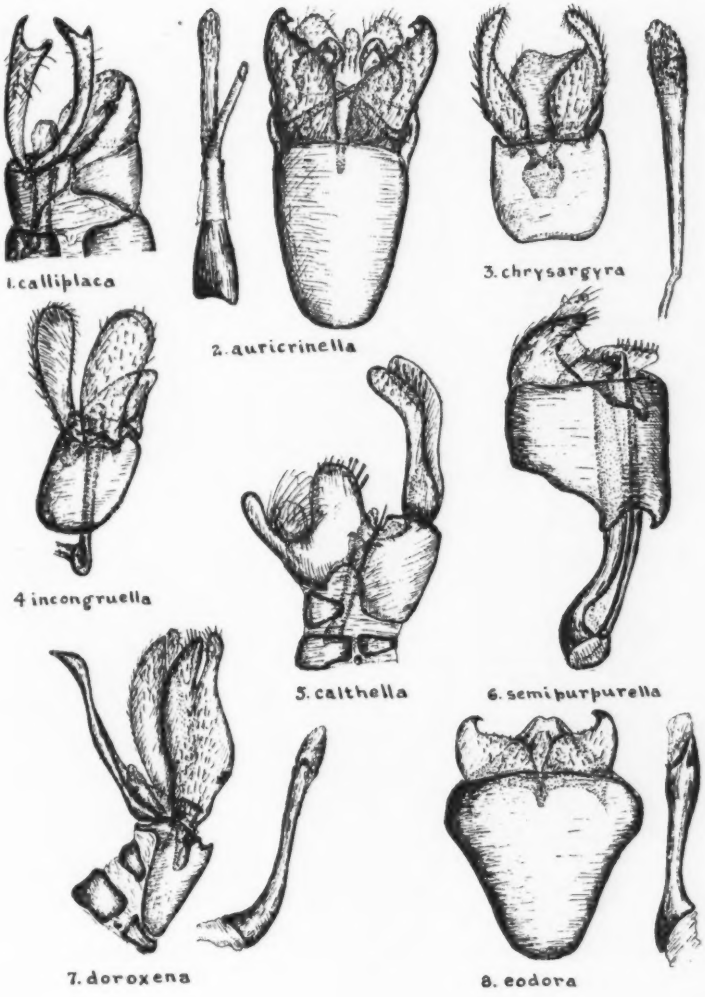

1 libania
2 eximius
3. thunbergella
4. petrosema
5. rothenbachii
6 sexnotatus
7. aruncella
8. intricata


1. calliplaca
2. auricrinella
3. chrysargyra
4 incongruella
5. calthella
6. semipurpurella
7. doroxena
8. eodora

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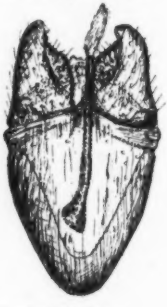
1. fastuosella

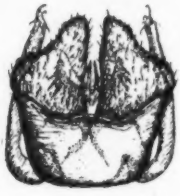
2. unimaculella

3. loxoscia

4. mediostriatella

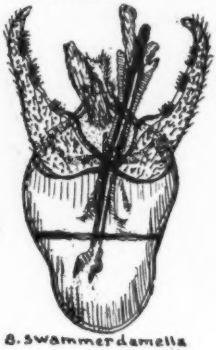


5. viridella



6. hamadelpha

7. septentrionella



8. swammerdamella

9. Wahlbergi

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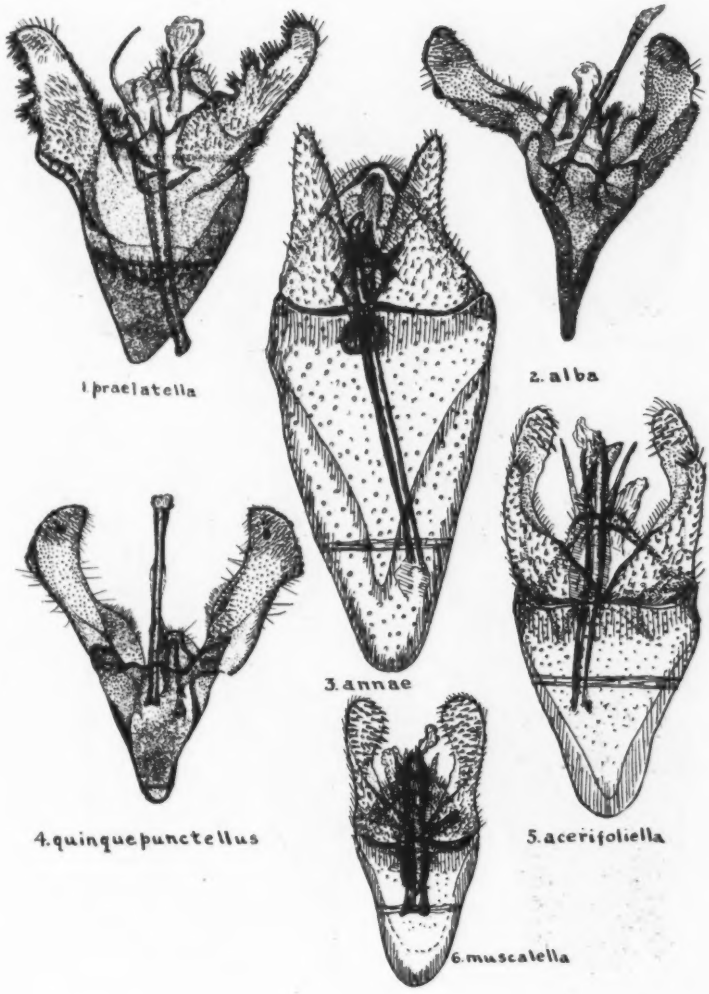
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2. alba
3. annae
4. quinquepunctellus
5. acerifoliella
6. muscalella

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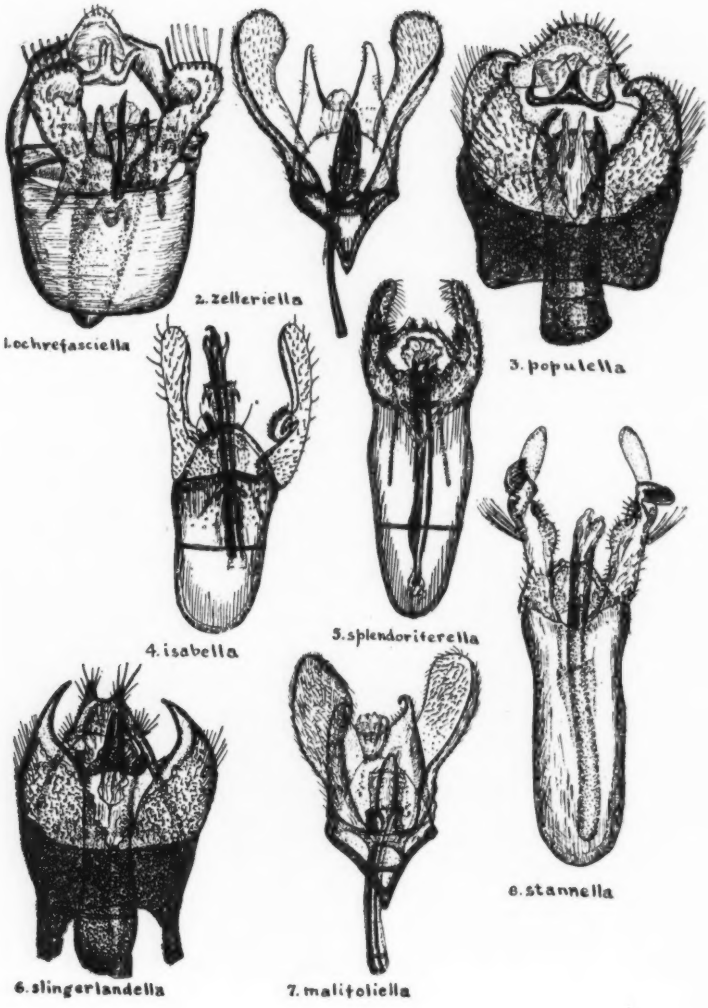
1. ochrefasciella
2. zelleriella
3. populella
4. isabella
5. splendoriferella
6. slingerlandella
7. malifoliella
8. stannella

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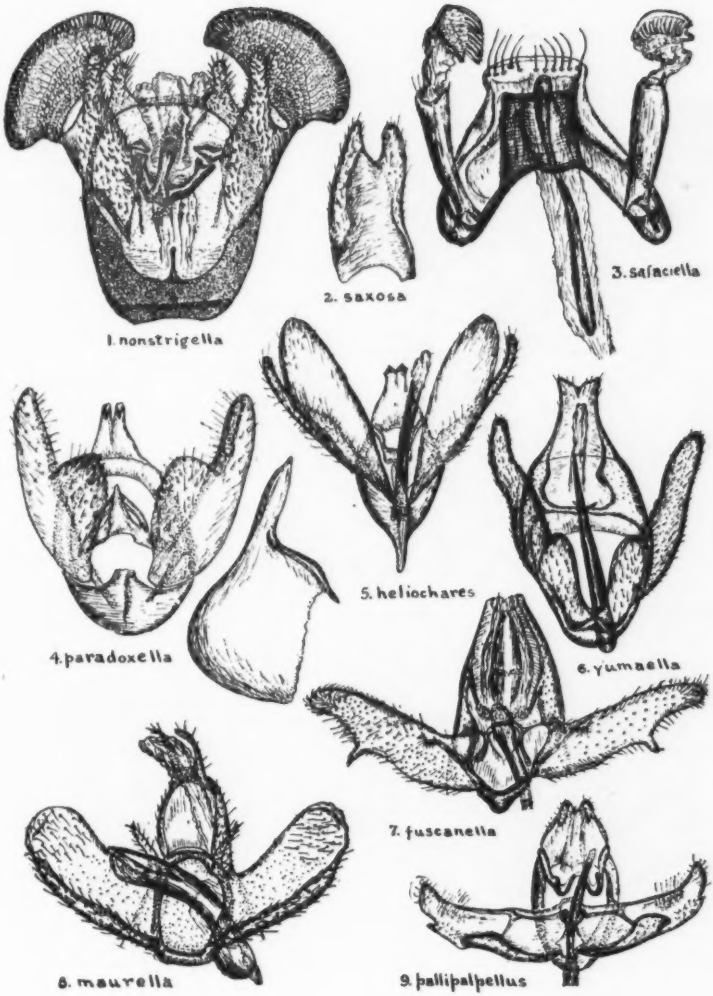
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2. saxosa
3. safnciella
4. paradoxella
5. heliochares
6. yumaella
7. fuscanella
8. maurella
9. pallipalpellus

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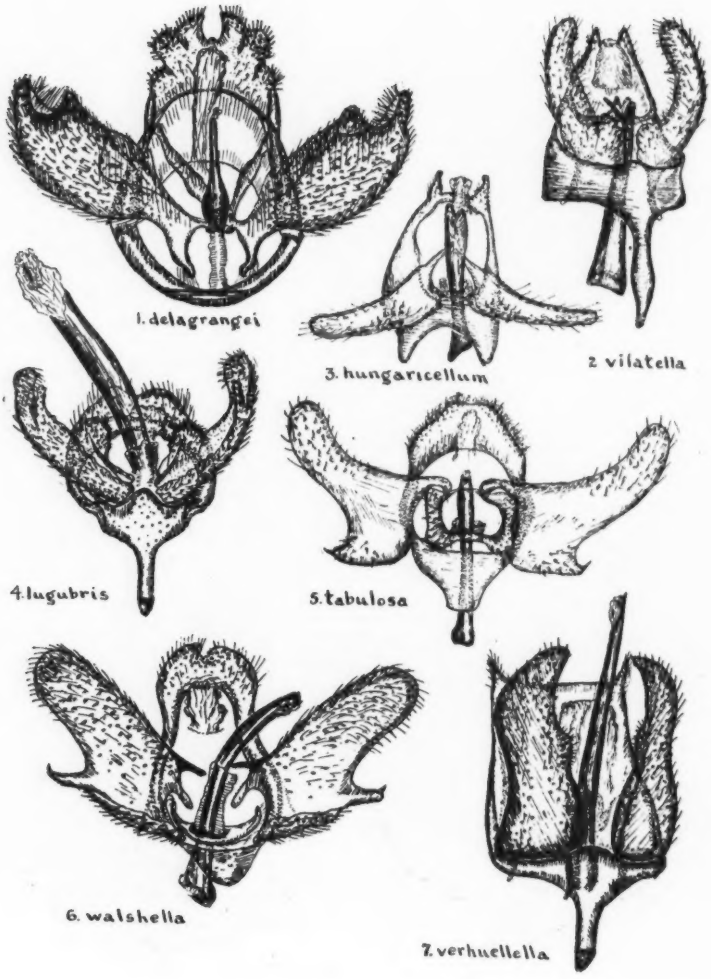
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3. hungaricellum
4. lugubris
5. tabulosa
6. walshella
7. verhuellella

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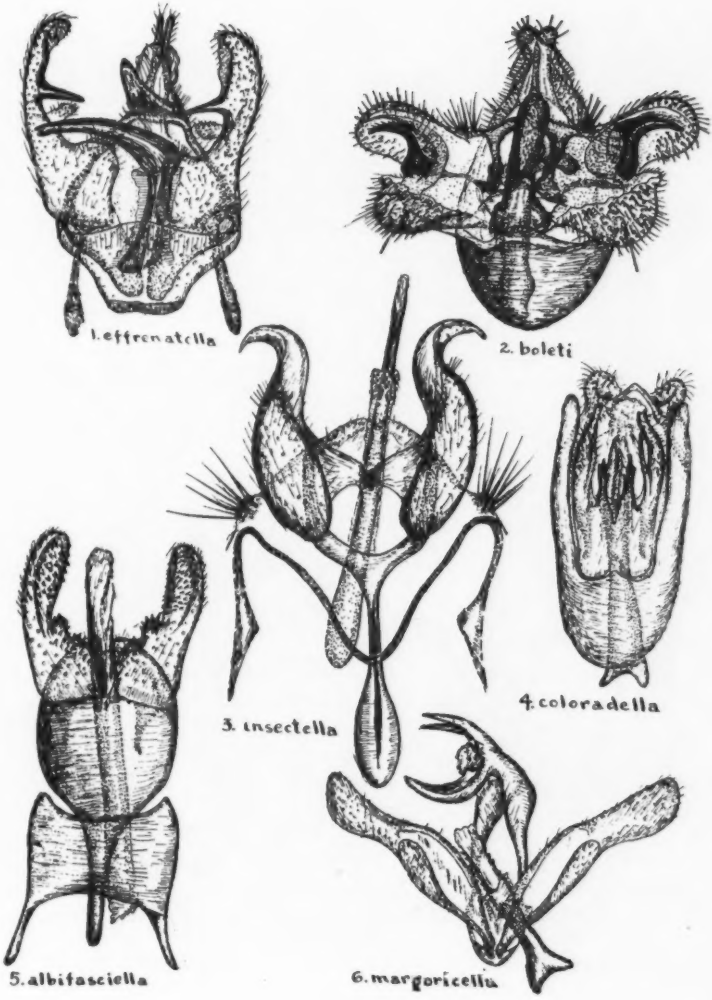
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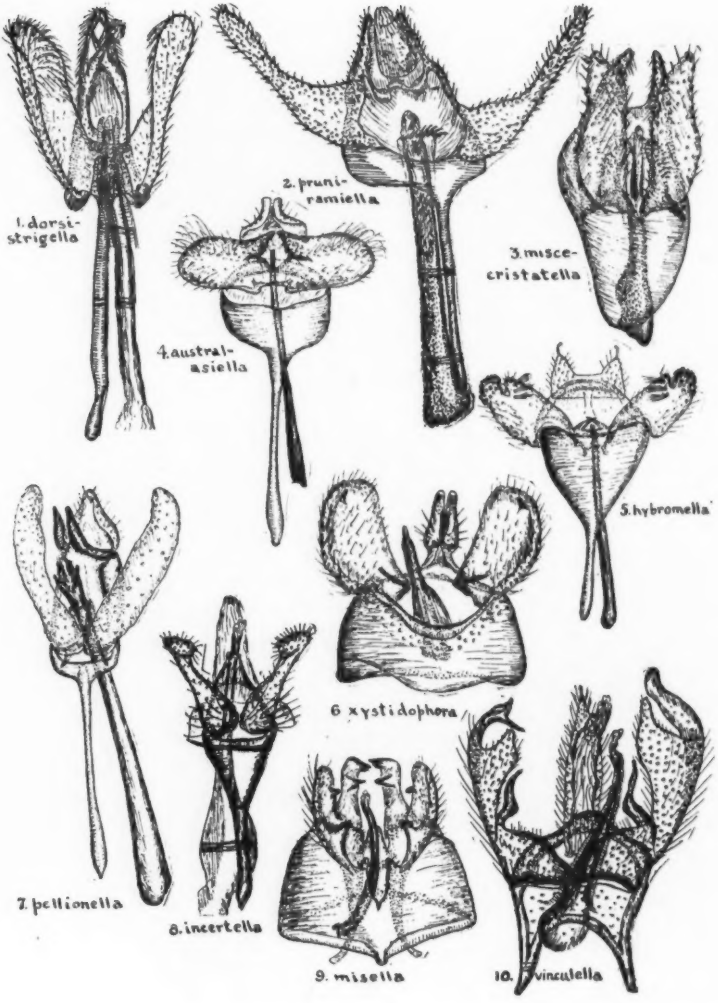
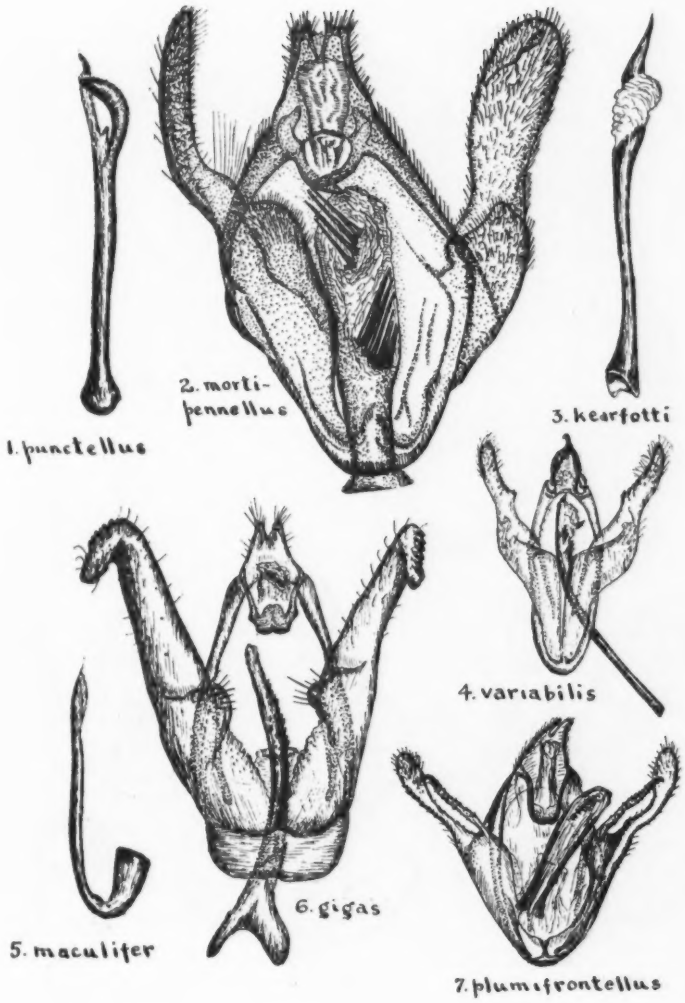
3. insectella
4. coloradella
5. albifasciella
6. margoricella


1. dorsi-strigella
2. pruni-ramiella
3. misce-cristatella
4. austral-asiella
5. hybromella
6 xystidophora
7. pellionella
8. incertella
9. misella
10. vinculella


1. punctellus
2. morti-
pennellus
3. kearfotti
4. variabilis
5. maculifer
6. gigas
7. plumifrontellus

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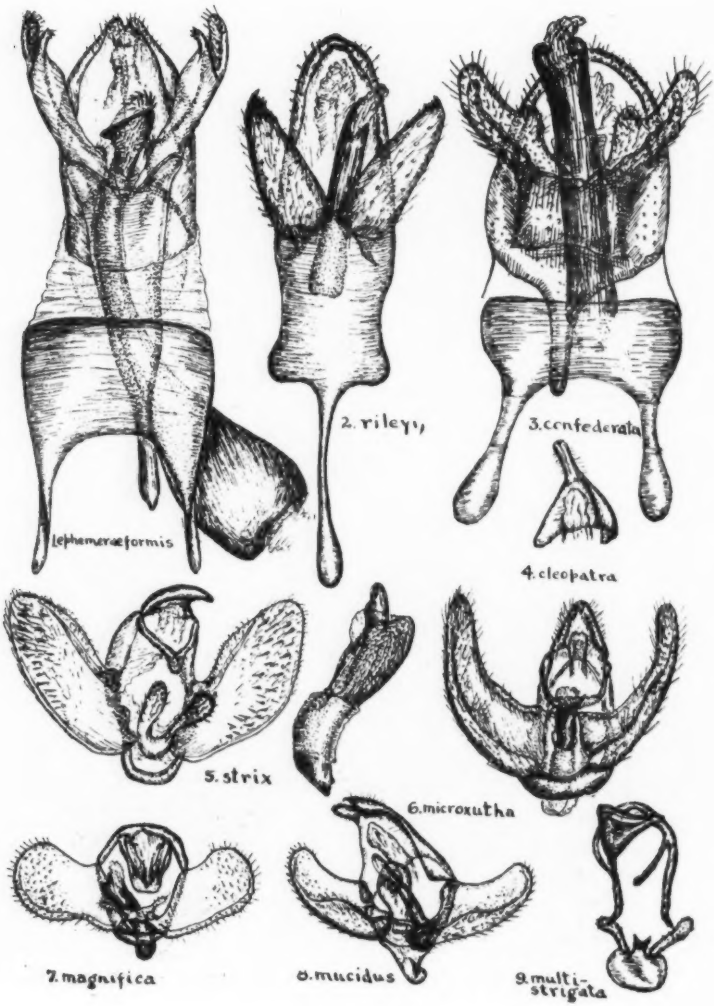
lephemeræformis
2. rileyi
3. confederata
4. cleopatra
5. strix
6. microxutha
7. magnifica
8. mucidus
9. multi-
strigata

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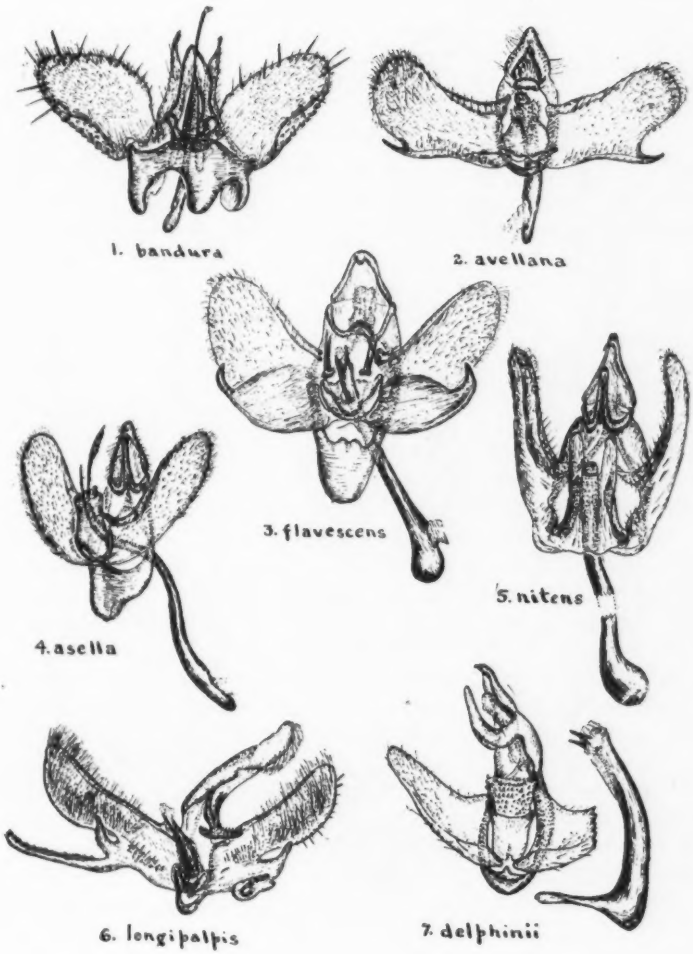
1. bandura
2. avellana
3. flavescens
4. asella
5. nitens
6. longipalpis
7. delphinii

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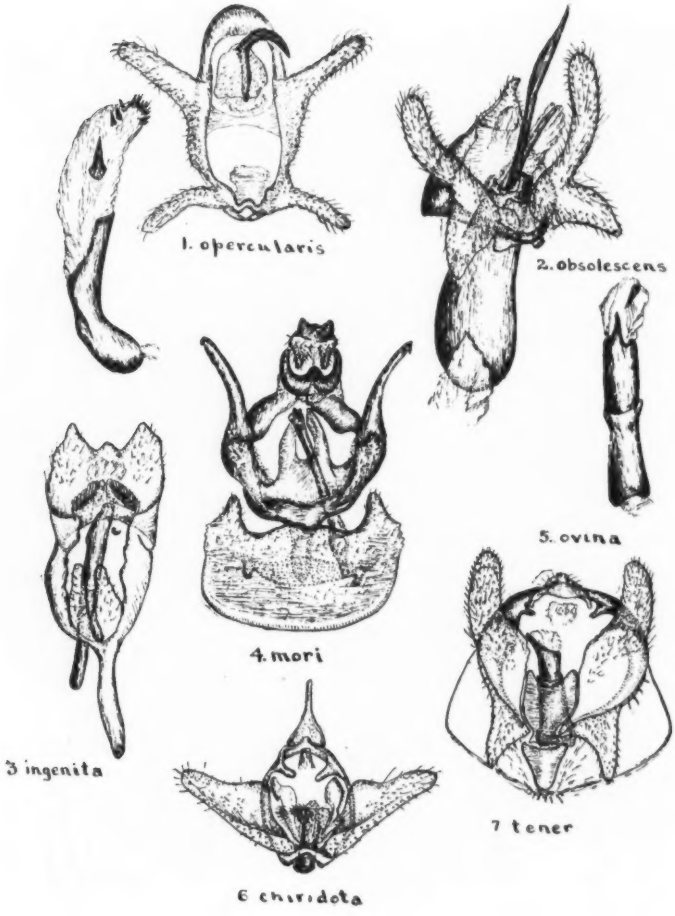
1. opercularis
2. obsolescens
5. ovina
4. mori
3 ingenita
7 tener
6 chiridota

John R. Eyer

THE EFFECT OF THE VENOM OF SOME SUPPOSEDLY POISONOUS ARTHROPODS.*

W. J. BAERG,
University of Arkansas.

CENTIPEDES.†

The centipedes, especially the larger species, are, according to popular opinion, dangerously poisonous. Stories regarding the effect of the bite of these arthropods may be gathered wherever they occur. A very common belief is that if the victim does not die, the flesh will rot and drop off from the region where the bite took place. To illustrate the reputation of the large centipedes belonging to the genus Scolopendra, the following story is cited. An officer in the Confederate army, while sleeping in his tent, was suddenly aroused by a creepy feeling on the chest. When a fellow officer had been awakened, and a light produced, a large centipede was found in the clothing of the officer and a number of spots of a deep red, forming a broad streak, indicated its passage across the chest and abdomen of the victim. Violent pain and convulsions soon set in, accompanied by excessive swelling in the bitten area. The victim fought with death for two days and then succumbed. The agony suffered by the bitten officer was described by an eye witness as the most frightful that he had ever observed.

Scientific writers, in want of any evidence to show either the dangerous or the harmless nature of centipedes, usually dispose of them with non-committal statements. Thus, Prof. Comstock (1) says: "The larger species, which occur in the warmer regions, are said to be extremely venomous." Herms (2) says that "in southern California the large greenish centipede, *Scolopendra heros*, is greatly feared. It is said that it not only punctures the skin with its poison claws, causing considerable pain, but also produces a reddish streak where it has crawled upon the body."

* Research paper No. 6, Journal Series, University of Arkansas.

† The various species of centipedes discussed here were determined by Dr. R. V. Chamberlain, Museum of Comparative Zoology, Cambridge, Massachusetts.

Pierce (4), after naming several species of centipedes which have been recorded as venomous (among these are four species of Scolopendra, including *S. heros*), goes on to say that "the centipede bite may cause some local pain, swelling, and erythema lasting a few hours. The general symptoms are great mental anxiety, vomiting, irregular pulse, dizziness, and headache."

Vorhies (6), of Arizona, describes two cases of a centipede bite. Unfortunately he does not give the name of the centipede involved, referring to it as "a large specimen." The symptoms that he gives are essentially those already quoted from Pierce, with, however, this qualifying statement: "Some of the symptoms given * * * may have been due to undue nervousness as to effects, as the victim in this case was undoubtedly somewhat wrought up about it."

Cornwall (4), who has made a study of one species of centipede (*Ethmostigmus spinosus*), believes that the venom principally serves as a digestive fluid. This, I believe, might well be applied to a number of species occurring in the United States.

The absence of definite experimental evidence regarding any species of centipedes makes a study of the effects of the poison of the small as well as the large species very desirable. For this reason, tests were made with the following species: *Lithobius mordax* Koch, *Theatops spinicaudus* Wood, *Scolopendra heros* Gir., and *Scolopendra polymorpha* Wood. The first three named are more or less common in Northwest Arkansas; the fourth was studied at State College, New Mexico. The effect of the bite of these species was tested on white rats, 4–5 weeks old, and on man.

Lithobius mordax is dark brown in color and about 20–25 mm. in length. It is very common in the Ozark region of Arkansas, and can be found readily under stones on hillsides and elsewhere.

On Rats. (3:00 P. M., April 2, 1923). The centipede, when put in position, readily bit through the skin of the inside of the leg; it was allowed to hold on for 8-10 seconds and was then removed by force. During the remainder of the day careful observation failed to reveal any effects of the poison on the rat.

On Man. Two days later (3:20 P. M., April 4, 1923), the same species of centipede was tried on myself. It was unable to puncture the skin on the inside of the small finger. The

mandibles barely caught in the cuticle. Another individual was tried, but this likewise failed to bite.

Theatops spinicaudus is light brown in color and an average specimen measures about 48 mm. in length. It is a rather active creature and quick to defend itself. This species is very common in Northwest Arkansas, though not so numerous as *Lithobius mordax*. It is found in the same situations as that species.

On Rats. (1:45 P. M., March 31, 1923). The centipede bit readily and vigorously. It had to be removed by force after it had held on for 8–10 seconds. The rat showed no signs of ill feeling, though it did lick the inside of the bitten leg a time or two. The punctures were clearly visible, but no sign of any inflammation or swelling appeared.

On Man. Several days later (3:25 P. M., April 2, 1923), this centipede was induced to bite me on the inside of the terminal joint of the small finger of the left hand. It bit well and was allowed to hold on for about five seconds, when it was forcibly withdrawn. The resulting pain was sharp, as if caused by a sharp needle. The poison, which gathered in two small drops near the punctures, is a clear liquid, with no clearly recognizable taste, perhaps slightly sweetish. In about 30 minutes all trace of the pain had disappeared. On the following morning the punctures could still be seen, but no inflammation or swelling appeared at any time.

Scolopendra heros apparently is rather common near Little Rock. It occurs in limited numbers in Northwest Arkansas near Monte Ne and Fayetteville. Limited experience indicates that it occurs in certain more or less restricted localities, where it can be found, at least during the warmer seasons, under stones and logs. The specimen used in the tests measured 135 mm. in length, inclusive of the caudal appendages. *Scolopendra heros* is a rather large species, having a greenish-black body, and light brown or yellowish legs. It is a very active and vigorous centipede that takes prompt action when one tries to interfere with its liberty. After a little practice it can be fairly well managed by the aid of cheese cloth (as large as a handkerchief or larger) and a dependable forceps.

On Rats. (9:00 A. M., July 8, 1923). The centipede bit eagerly and was withdrawn with considerable effort when the fangs had been inserted for 4–5 seconds. The rat held the

bitten leg well off the floor of the cage and the stare in its eyes suggested considerable pain. For about thirty minutes these symptoms continued and the rat showed little interest when prodded with a pencil. About five minutes later the rat again became alert and the stare in the eyes disappeared. The punctures appeared as small red spots; there was no evidence of swelling or inflammation. The sore feeling in the bitten leg remained for some time, as shown by unnatural positions in which the rat would rest, by keeping eyes half closed, and by lifting up and frequent licking the wounded leg. In about 5 hours (2:20 P. M.) these symptoms disappeared and the rat was, according to all indications, quite normal.

On Man. On the following day (7:55 A. M., July 9, 1923), the *S. heros* was induced to bite me on the inside of the distal joint of the small finger of the left hand. After a few unsuccessful attempts the fangs were well inserted, and were allowed to remain about 4 seconds. The pain immediately following, and later, is sharp and strictly local. There is nothing in the nature of an ache. For 15 minutes the sensation remained about the same, then it began to decrease quite noticeably. At this time a faint white disk appeared near the punctures, resembling, but not nearly as distinct, as that following a bee sting. In about two hours (9:55) the pain had become very slight, but there was a slight general swelling in the small finger, giving it a "puffed up" appearance that was readily noticeable. Three hours after the bite took place the pain could be felt only when pressing upon the punctures. This, too, disappeared during the course of the day.

Scolopendra polymorpha, according to Dr. R. V. Chamberlain, "is the common species in California and occurs west into Texas, etc." The legs of this species are light yellow, the segments of the body are somewhat darker and at their posterior margin they are blackish. The head and nearby segments of the body are reddish brown, as are also the antennæ. The specimen used in the tests, apparently somewhat larger than the average, measured 145 mm. in length, including the caudal appendages.

In habits and behavior this species resembles very closely *S. heros*. In the southern part of New Mexico* (State College,

*Prof. R. F. Crawford, of State College, New Mexico, rendered much valuable assistance both in securing specimens of centipedes and scorpions and in making various tests.

Aden, and Deming) specimens are most easily secured by turning over the old fallen Yucca stems that occur in considerable numbers in restricted localities. This species burrows rather well, and with some careful study distinctive characters of its burrow could probably be found. With this information at hand, these centipedes could probably be found in considerable numbers almost anywhere within the region of their distribution. *Scolopendra polymorpha* was the only large species of centipede that I was able to get while at State College, New Mexico.

On Rats. (8:10 A. M., September 17, 1923). The centipede bit as soon as it had been conveniently placed, and after about five seconds was removed with considerable difficulty. The rat held up the leg for a short while, then favored it when walking. It remained quite alert, eyes wide open, and took some food that was supplied. After about 3 hours (11:00 A. M.) the rat no longer even favored the leg, and appeared to be entirely normal. The punctures (on the inside of the left hind leg) were clearly visible, but there was no inflammation or swelling.

On Man. Two days later (7:45 A. M., September 19, 1923), the same centipede used above was induced to bite me on the inside of the terminal joint of the small finger. It inserted its fangs twice, and the second time it held on so tenaciously that I was obliged to loosen it with the aid of a pair of forceps. The fangs remained inserted for 4–5 seconds. Small drops of the poison, a clear liquid, gathered over the punctures. The resulting pain was sharp, like that following the prick of a needle. It was quite marked, but not severe. It remained noticeable, though gradually growing less, till in a little over three hours (9:55) it had practically disappeared. Near the punctures there appeared small drops of perspiration; there was no distinct reddening, no clearly visible white area, nor perceptible swelling.

One symptom that I had not observed from the bites of other centipedes was the sensation in the bitten area suggesting that a very fine splinter, or several of them, had been left in the punctures. This feeling was very marked whenever the bitten finger was gently pressed, and it remained all through the day. This feature has already been mentioned by Vorhies.

The Poison Glands. It seems that these glands have been but little studied, and it may therefore be appropriate to add to the observations on the effect of the poison a few figures and a brief description of the glands. The poison glands are located in the basal segments of the first pair of legs, which are modified

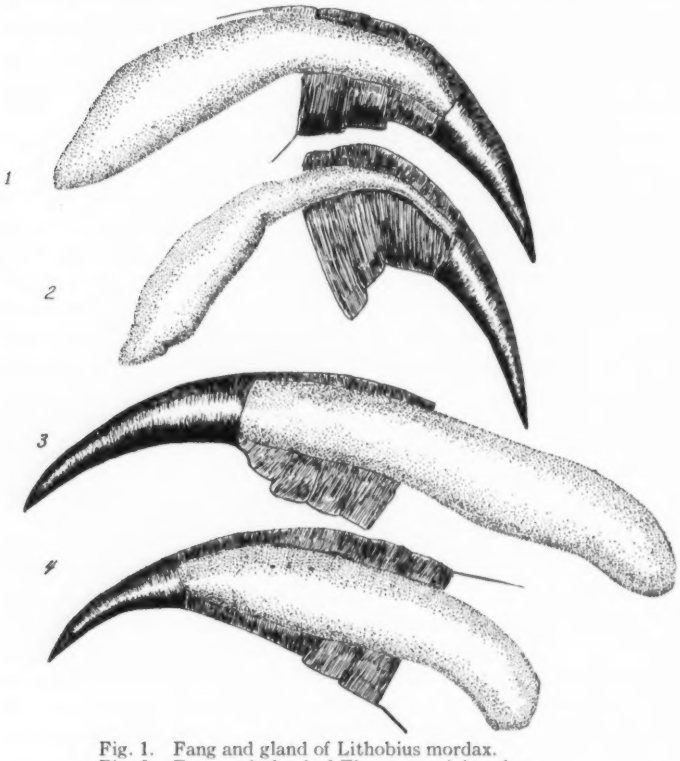

Fig. 1. Fang and gland of Lithobius mordax.
Fig. 2. Fang and gland of Theatops spinicaudus.
Fig. 3. Fang and gland of Scolopendra heros.
Fig. 4. Fang and gland of Scolopendra polymorpha.

into fangs that are used for seizing and holding prey. The distal portion of the fangs is hard and firm and the glands open through a small sunken slit-like opening located dorsally near the tip. The measurements of the length of a gland were taken from the basal or rigid and hard part of the fang where the gland tapers into a duct, to the farther end of the gland.

In *Lithobius mordax* the gland measures 1.35 mm. in length, from the base of the fang, i. e., at the first joint, and .4 mm. at its greatest width, (Fig. 1). The poison gland of *Theatops spinicaudus* is 1.5 mm. in length and .5 mm. in width, (Fig. 2). The poison gland of *Scolopendra heros* is 3.5 mm. in length and .8 mm. at its greatest width, (Fig. 3). The poison glands of *S. polymorpha* are slightly larger; length 4 mm. and the greatest width 1 mm. (Fig. 4).

SCORPIONS.*

Although some folks regard scorpions as rather dangerous, the general opinion regarding the species occurring in the United States is that the effect of their sting is no worse than that of a wasp or honey bee. There appears to be very little, if any, experimental evidence to support this opinion. Scorpions are very numerous in Northwest Arkansas. They may be found on stony hillsides or other relatively dry or welldrained situations. During the day they may be observed under stones or logs, etc. The common local species is *Centruroides vittatus* Say.

The usual method of experimentation was not followed here, because the effect of the venom of the local species is known to be relatively harmless. It was not necessary to try the venom on myself, because a student in the class in Nature Study, while on a field trip, offered to take the test. His offer was promptly accepted and the test (on the first finger of the left hand) was made at once. The sting of the scorpion produced in a very short time a white area immediately surrounding the punctures, very much like that following a bee sting. The pain was rather sharp and severe at first, then growing somewhat more dull and accompanied by an aching sensation proceeding along the forearm. In about an hour the pain had practically disappeared. There was no swelling or other symptom.

According to a report by Dr. H. V. Jackson (3), published in the Interstate Medical Journal, a certain species of scorpion (*Centrurus exilicauda*) near Durango, Mexico, causes from 51 to 53 deaths annually. It seems that as a rule the poison does not cause death; but in many cases the symptoms are rather severe. Dr. Jackson was stung in the palm of the hand and for several weeks the particular "side of the body was numb and

*The scorpions discussed here were determined by Dr. H. E. Ewing of the U. S. National Museum.

without muscular sensation." In view of a possibility that some of the scorpions in southern New Mexico might produce similar symptoms, I secured a number of specimens. So far as could be determined at the time, all belonged to the same species, *Vejovis spinigerus*.

On Rats. (8:10 A. M., September 22, 1923). The scorpion used in the test stabbed the rat two or three times, and appar-

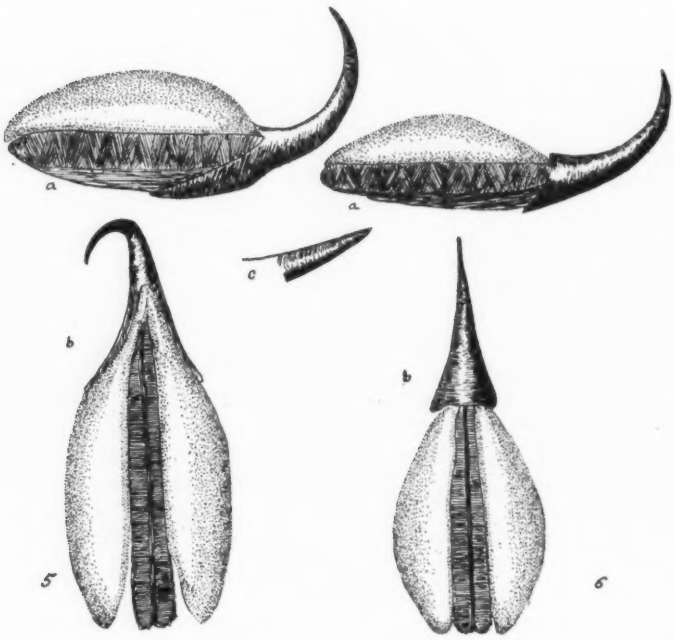

Fig. 5. Spine and glands of Centruroides vittatus.
a, side view; b, ventral view; c, side view tip of spine showing opening.

Fig. 6. Spine and glands of Vejovis spinicaudus.
a, side view; b, ventral view.

ently caused considerable pain. When put back in the cage the rat licked the inside of the leg rather energetically. In walking it did not seem even to favor the leg. It was quite alert in every way and appeared to be entirely normal. Observation throughout the day failed to show any symptoms of poisoning.

On Man. A few days later (8:00 A. M., September 25, 1923), the scorpion was allowed to sting me on the inside of the small finger of the left hand. It stabbed quickly two times, so that a bit of blood gathered in the punctures. The sensation was very much like that of a pin prick, and the resulting pain, which was very slight, lasted scarcely a half an hour. There was no white area around the punctures and not the slightest swelling or inflammation.

The poison glands. A careful study of the poison glands of an exotic species has been made by H. F. Wilson (5). Since

Fig. 7. Near Deming, N. M. Abundant yucca stems make a favorable collecting ground for centipedes.

the native species apparently have not been studied, it seemed desirable to add to the observations on the effect of the poison a brief description and some illustrations of the glands.

Centruroides vittatus. As already described by Wilson (in *Prionurus citrinus*), the two glands, located in the last segment of the abdomen, are covered on their mesal and dorsal aspects by a layer of muscle. Each gland measures 3 mm. in length, .8 mm. at its greatest width, and .75 mm. at its greatest depth. The general appearance of the poison apparatus is shown in Figures 5 and 6. The glands open through two pores located laterally near the tip of the sting.

Vejovis spinigerus. This species, common in southern New Mexico, is somewhat smaller than our local form. The glands are essentially like those already described. They measure 2.75 mm. in length, and .7 mm. at the greatest width.

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A NEW SPECIES OF THE MEALY-BUGS.*

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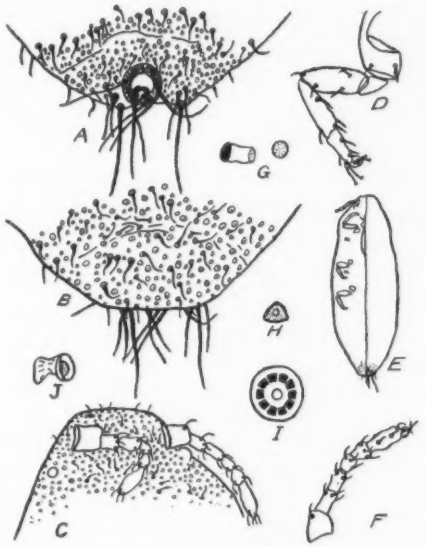
The writer collected the specimens of this mealy-bug from a nest of the ant Lasius. This nest was under a rock in an open grassy place near the Chautauqua grounds at Boulder, Colorado. Apparently it was a new species belonging to the genus Trionymus.



Trionymus hypolithus n. sp.

A, Adult female, apex of abdomen, dorsal, X160. B, Same, apex of abdomen, ventral, X160. C, Same, anterior portion of body, X160. D, Same, metathoracic leg, X160. E, Same, outline of body. F, Same, antenna, X160. G, Same, tubular duct and opening, X1520. H, Same, triangular pore, X1520. I, Same, multilocular disk pore, X1520. J, Same, spiracle, X160.

After a careful search of available literature on the subject and failure to find specific descriptions corresponding to the characters of the insect, specimens were forwarded to Mr. Harold Morrison, U. S. Bureau of Entomology, Washington, D. C. His reply was a belief that the specimens represented a new and undescribed species of the genus Trionymus.

*Order Hemiptera, Family Coccidæ, Subfamily Dactylopiinæ.

So far only two specimens have been collected and both have been mounted. Therefore, the following description is made from these two mounted specimens:

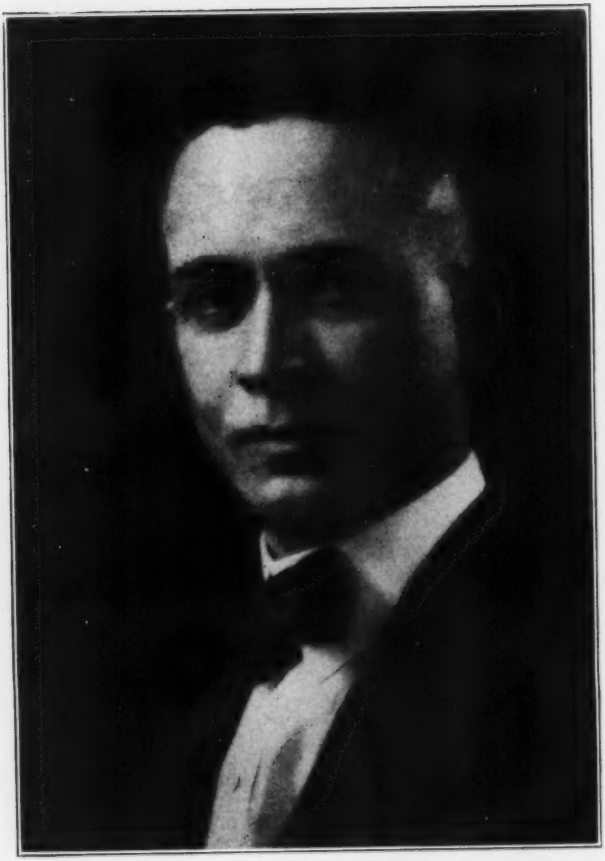
Adult female: Body elongate, being about three times as long as wide; length approximately 1.54 mm. and width about 0.59 mm.; the sides are sub-parallel; both anterior and posterior ends of the body truncate; with the usual two pairs of spiracles; specimens stain a dark pink in fuchsin due to the numerous derm pores; both dorsal and ventral surfaces thickly covered with short, broad tubular ducts, triangular pores, and large prominent multilocular disk pores; the segments of the body are clearly defined due to the band-like arrangement of these derm pores; the dorsal setæ are few, short and flagelliform; on the ventral surface the setæ are also flagelliform but more numerous, of varying lengths and as a rule longer than the dorsal body spines; two labiate structures are found on the dorsal surface of the abdomen, laterad to the median line, between the second and third segments from the apex; antennæ 6-jointed, ordinary, fairly close together; the distance between the bases of the antennæ approximately 150 microns; the range of measurements in microns of the segments in two individuals is as follows: 1, 37–41; 2, 35–39; 3, 39–45; 4, 26–26; 5, 30–35; 6, 67–75; eyes located just posterior to the bases of the antennæ; the beak is 2-jointed, short, blunt and broadly triangular; length approximately 91 microns, width (proximal end) 90 microns, with several setæ on the distal end numbering from 12 to 14; legs normal, fairly stout, claw without denticle, digitules longer than claw and knobbed, setæ somewhat numerous on tibia and tarsus; the range of measurements of the segments of the legs in microns is as follows:

	Coxa	Trochanter Plus Femur	Tarsus	Tibia Without claw
Prothoracic leg.....	43—46	155—162	94— 97	67—73
Mesothoracic leg.....	45—47	152—163	97—103	69—75
Metathoracic leg.....	45—50	161—172	110—112	75—84

Only one pair of cerarii discernible and those are on the anal lobes; each with three cerarian spines which are setiform and much longer than the body setæ; one of these three is twice as long as the other two being greater in length than the anal ring hairs; no grouping of pores about the cerarii; anal lobes fairly defined, with cerarii, auxillary setæ, short, broad, tubular ducts, triangular pores and multilocular disk pores; anal ring with six hairs, each approximately twice the diameter of the anal ring itself; both the dorsal and ventral apical portions of the abdomen covered with numerous long setæ giving a rather hairy appearance to the posterior end of the body.

Immature stages: None available for examination.

Adult male: No specimens collected.



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